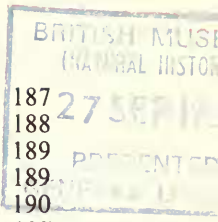
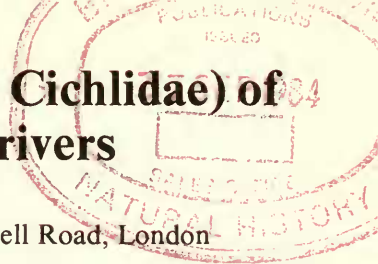


# The haplochromine species (Teleostei, Cichlidae) of the Cunene and certain other Angolan rivers

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## Introduction

*L'Angola est un plateau d' où descendant de nombreux fleuves et rivières qui cachet encore bien des secrets* Poll (1967:16)

Despite Poll's (1967) extensive monograph on the fishes of Angola, and the work of Trewavas (1964, 1973) and Bell-Cross (1975) much has still to be learnt about the biology, taxonomy and zoogeography of the haplochromine cichlid species in this region of Africa (see Greenwood, 1979). A basic inventory of the species has been worked out, but many taxa are known only from the type specimen, by a limited number of type specimens or by some specimens whose locality is recorded no more precisely than 'Angola'. Above all, almost nothing is known about the phyletic relationships of the species, and hence zoogeographical conclusions based on them are correspondingly uncertain.

Judging from the present-day hydrography of Angola, especially the isolated rivers which discharge directly into the Atlantic, and the numerous tributaries emptying into the Zaire system, one might expect a high degree of localized endemism in the various rivers. In other

words, the physical background would seem ideal for promoting vicariant speciation, a situation that is, indeed, suggested by some of the taxonomic data already available.

Thus it was with considerable pleasure and interest that I accepted an invitation from Dr M. Penrith (then of the Windhoek Museum) to study a large collection of cichlid fishes from, principally, the Cunene river. The Cunene is one of the least studied Angolan rivers, and physiographically is one of the most isolated in the country. The collection has provided an opportunity to redescribe a number of species on the basis of many more specimens than were previously available, and to confirm the presence in the Cunene of species either not previously recorded from there or recorded with some uncertainty. Also, it has established that several species have an extensive distribution within the river itself, their ranges stretching from or near the river mouth, almost to its northernmost tributaries.

Less has been learnt about the relationships of the endemic Cunene species, and the collection has underlined the still unsatisfactory taxonomic situation surrounding species of the *Serranochromis* subgenus *Sargochromis*. However, a species currently of indeterminable status '*Haplochromis*' *welwitschii* (Blgr), whose type specimen is probably from the Cunene, can now be referred to the genus *Chetia*, a taxon otherwise known from the Limpopo system in South Africa (see Appendix II), and a tributary of the Zaire system (see Balon & Stewart, 1983). In terms of species numbers and morphological diversity, the Cunene seems to have a haplochromine fauna more complex than that in any other Angolan river and, indeed, more diverse than that of the Zambezi-Kafue systems. The new collection also apparently corroborates existing ideas that the Cunene fauna, on a broad zoogeographical scale, has phyletic affinities with both the Zaire and the Zambezi drainage systems (Trewavas, 1964, 1973; Bell-Cross, 1975; Roberts, 1975). However, sister-group relationships for the endemic haplochromines both within and outside the different systems still cannot be established. Zoogeographical problems are compounded by the fact that precise specific identification is impossible for most Cunene representatives of the *Serranochromis* (*Sargochromis*) species complex, and is unlikely to be obtained until more specimens, coupled with data on male breeding colours, are available from the different river systems within and outside Angola.

### Methods and materials

**Methods.** Measurements and counts generally are those used in my other papers on haplochromine fishes (see Greenwood, 1981). Measurements relating to the neurocranium are those used in Greenwood (1980: 4–6); an additional measurement used here, ethmovomerine length, is taken directly from the anterior tip of the vomer to the most ventrolateral point on the lateral ethmoid bone.

When the length of the ascending premaxillary process is given for whole specimens it is measured directly from the dentigerous surface of the bone, between the teeth on either side of the midline, to the distal tip of the processes (determined through the skin by moving the premaxillae gently forwards and downwards). When this length is taken from a skeletal preparation, the depth of the dentigerous arm is excluded, and the reference points are those illustrated in Greenwood (1980: 5, fig. 2), viz from the distal tip of the processes to a horizontal line drawn level with the upper margin of the dentigerous arm immediately posterior to the basal region of the ascending processes.

Measurements of the lower pharyngeal bone are those employed by Bell-Cross (1975: 410), viz: length is taken along the median axis of the bone, from the anterior tip of its shaft to a line drawn transversely between the tips of the posterior horns. Lower pharyngeal breadth is measured directly between the outer edges of the two horns.

A feature not previously mentioned in the description of haplochromine species is the *anal sheath scales*. My attention was drawn to these scales when examining part of the type series of *Tilapia steindachneri* Blgr (see p. 190). In these specimens, a distinct but shallow sheath of small, almond-shaped scales, aligned in a single row, lies between the anal fin base and the ventral row of body scales. The long axes of the scales are arranged horizontally, and the scales are either imbricate or spaced, sometimes widely spaced.

It seems that anal sheath scales occur in a number of haplochromine lineages. A sheath, or at least some characteristically almond-shaped scales, has been found in species from Lakes Victoria, Tanganyika and Malawi, as well as in some fluviatile taxa. Sheath length varies intraspecifically to a considerable extent. It can be present along almost the entire base of the fin, or it may be confined to the base of the spinous part (apparently the commonest condition). Often it is represented merely by a few isolated scales. Since the scales are easily dislodged, the latter condition may be artefactual.

The taxonomic value of the anal sheath, in whatever form it is present, cannot yet be assessed.

**Materials.** All the type specimens of Angolan haplochromine species in the BM(NH) collections were examined, as were other specimens identified as conspecific with these types or with type specimens of Angolan species held in other institutions. Likewise, all the BM(NH) material of *Serranochromis* and *Pseudocrenilabrus* species was studied, together with the type and other specimens of '*Haplochromis*' *darlingi*, a species first recorded from Angola by Poll (1967).

In addition, the following material was borrowed from the Zoological Museum of Hamburg (ZMH) and the Musée Royal de l'Afrique Centrale, Tervuren (MRAC).

ZMH 4599 *Haplochromis* species (7 specimens) Cunene R.

4599a *Haplochromis* species (1 specimen), Cunene R. at Capelongo.

1300 *Serranochromis angusticeps* (1 specimen), Cunene R. at Capelongo.

1307 *Serranochromis angusticeps* (1 specimen), Cunene R. at Capelongo.

1718 *Serranochromis robustus jallae* Cunene R. at Mülongo Fürt.

1719 *Serranochromis thumbergi* (2 specimens) Cunene R. at Capelongo.

The identity of all these *Serranochromis* specimens has been confirmed.

1722 *Haplochromis frederici* (4 specimens), Cunene R. at Capelongo. Two specimens are members of the *Serranochromis* (*Sargochromis*) *giardi-codringtoni* complex (see pp. 217–224 below), and two probably can be referred to *S. (Sargo.) coulteri* (Bell-Cross).

Musee Royal de l'Afrique Centrale (MRAC), Tervuren.

MRAC 154779–780 *Haplochromis welwitschii*, Sanguenque Uembe Cûanaa, Angola.

MRAC 66470 *Haplochromis schwetzi*, holotype, Cuango R., Angola.

MRAC 163992; 164013–016; 164023–026; 164027–032; 164033–39 *Haplochromis schwetzi*, paratypes (26 specimens), Cuango R., Angola.

MRAC 163981–986 *Haplochromis darlingi*, Lac Calundo, Angola.

Other material examined is listed in the text. Regrettably, as a result of extensive reorganization now been carried out in the fish collections of the Vienna Museum, it was impossible to examine the types of two Steindachner (1866) species: *Chromis humilis* and *Chromis acuticeps*. Both taxa are described, simply, as coming from Angola. Fortunately the types of both species were carefully examined by my colleagues Dr Ethelwynn Trewavas, and later by Mr G. Bell-Cross (now of the Port Elizabeth Museum, South Africa). I have been able to use the notes and recollections of both these people, to whom I am most indebted.

## The haplochromine species of the Cunene river

### *THORACOCROMIS* Greenwood, 1979

Several Angolan species, currently referred to the genus *Haplochromis*, show the diagnostic features of *Thoracochromis*, viz an abrupt size change between the small scales on the chest and the larger scales on the ventrolateral aspects of the flanks, a marked anteroventral embayment of the cheek squamation (with, in some species, a narrow, horizontal naked area lying between the cheek scales and the preoperculum), and the absence of true ocelli, but not discrete spots, on the anal fin or adult males (see Greenwood, 1979: 290–292).

The Angolan species now placed in *Thoracochromis* are: *Haplochromis lucullae* (Blgr), 1913; *H. albolabris* Trewavas & Thys van den Audenaerde, 1969; *H. schwetzi* Poll, 1967, and *H. buysi* M.-L. Penrith, 1970.

*Haplochromis lucullae* was treated as a junior synonym of *H. acuticeps* (Steindachner, 1866) by Regan (1922: 255), but the species has been informally 'resurrected' by several recent authors, notably Trewavas (1964: 8-9, 1973: 31), Penrith (1970: 170-171) and Bell-Cross (1975: 427). Unfortunately, I have not been able to examine the holotype of *H. acuticeps* (see p. 189) but from Dr Trewavas' comments, based on detailed examination of that specimen, its separation from *lucullae*, at least at the species level, is justified (see also Trewavas, 1973: 31). Regrettably, neither Steindachner's (1866) original description, nor Trewavas' later reexamination of the *acuticeps* type specimen provide any information on the nature of the size-change at the chest-abdominal scale transition line, nor are there data on the nature of the cheek squamation. Thus it is impossible to comment on the generic assignment of '*acuticeps*'. Steindachner's figure, however, suggests that the scale transition is of the *Thoracochromis* type.

With one exception (*Th. schwetzi*), and unlike species of *Thoracochromis* from the Nile, Lake Turkana and the Zaire river system, none of the Angolan species has more than 4 or 5 upper lateral line scales each separated from the dorsal fin base by one large and one small scale. This low number is thought to represent the primitive condition, the higher number (8 or 9 scales) occurring in the other species being the derived one (Greenwood, 1979: 291). As compared with the Nilo-Zairean taxa most Angolan species have more scales in the lateral-line series and higher modal counts for this feature. Again, an exception is *Th. schwetzi*, whose lateral line counts are like those in the Nilo-Zairean species; interestingly, *Th. schwetzi* occurs only in the Cuango river, an Angolan affluent of the Zaire system.

In all other meristic and morphometric features the Angolan *Thoracochromis* do not lie outside the range of variability found in other members of the genus. The significance, if any, of the differences in squamation cannot be assessed until more data are available from those Angolan species which are currently represented only by one or a few type specimens.

Species previously referred to *Haplochromis* and which are not members of *Thoracochromis*, are discussed in Appendix I.

### *Thoracochromis buysi* (Penrith), 1970

SYNONYMY *Haplochromis buysi* Penrith, M.-L., 1970. *Cimbebasia*, ser A, 1 (7): 168-171, plate 2; fig. 1. Holotype: SM5099, a specimen 75 mm standard length, from the Cunene river mouth.

Paratype: SAM 25243, a specimen 61 mm SL from the same locality. This specimen is now damaged extensively, and was not used in the redescription of the species. It is, however, conspecific with the holotype.

*Tilapia steindachneri* (part) Boulenger, 1913. *Ann. Mag. nat. Hist.* (8) 12: 483. Five of the syntypical specimens only (BMNH 1907.6.29:141-5, from the Que river). The largest specimen, 104.5 mm SL, alone is in reasonable condition. Although Boulenger (1913) did not select a holotype, he did later (1915) designate one specimen as 'Type' in the caption to a figure of that specimen. The fish in question is one of the syntypes from Mossamedes which Regan (1922) included in the species *Sargochromis mellandi*. Thus the inclusion of the five Que fishes in the synonymy of *Thoracochromis buysi* (Penrith), 1970 raises no question of nomenclatural priority for Boulenger's earlier name '*steindachneri*'.

*Haplochromis acuticeps* (part): Regan, 1922. *Ann. Mag. nat. Hist.* (9) 10: 255 (the syntypical specimens of *T. steindachneri* noted above; BMNH 1907.6.29:141-5).

DESCRIPTION. Based on 46 specimens, including the holotype, 44.0-118.0 mm standard length.

Depth of body 29.4-34.7 (M=32.0)% of standard length, length of head 30.4-36.4 (M=31.5)%.

Dorsal head profile gently curved (almost straight in a few specimens), sloping at an angle of 35°-40° to the horizontal, the angle increasing with the fish's size. The upper margin of

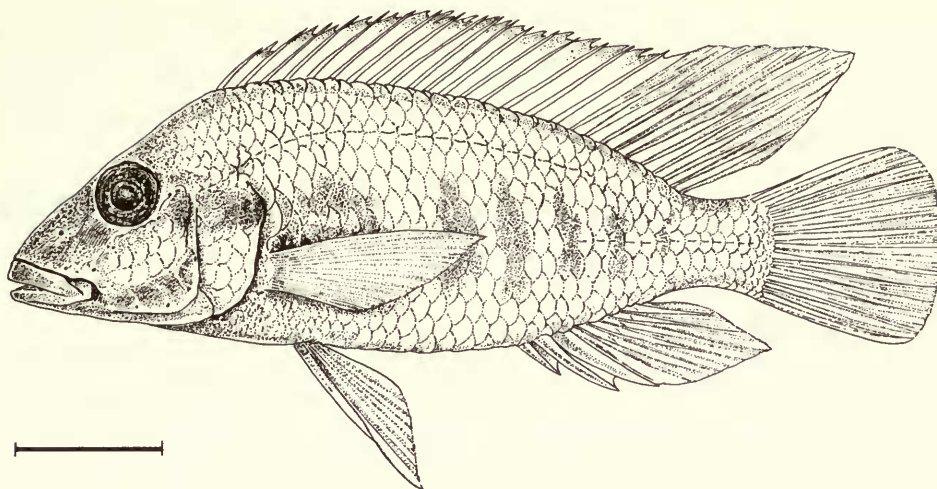


Fig. 1 *Thoracochromis buysi*. Adult male (1984.2.6: 24). Drawn by G. J. Howes. Scale = 20 mm.

the eye is coincident with, or lies immediately below the dorsal profile of the head, but never extends above it. The extent to which the curve of the profile is interrupted by the intrusion of the premaxillary ascending process varies, but is never marked and may be influenced by preservation methods.

Preorbital depth 18.5–26.0 ( $M=22.9$ )% of head length, showing slight positive allometry with standard length; least interorbital width 16.6–23.6 ( $M=19.4$ )% of head. Preorbital depth is generally greater than least interorbital width, but in some individuals the measurements are equal; in no specimen examined is the interorbital width greater than the preorbital depth (cf. *Th. schwetzi* where the interorbital is wider than the preorbital is deep).

Snout length shows clear cut allometry with standard length. The range for the whole sample is 31.0–39.0% of head; in specimens less than 70 mm SL ( $n=17$ ) it is 31.0–35.3 ( $M=33.1$ )% and in larger individuals (71.0–118.0 mm SL,  $n=29$ ) it is 34.5–39.0 ( $M=36.7$ )%. The snout is from 1.0–1.3 times longer than broad (modal range 1.0–1.1).

Eye diameter is negatively allometric with standard length; for the whole sample it is 25.4–36.2% of head length, in fishes < 70 mm SL it is 28.6–36.2 ( $M=33.6$ )%, and in larger individuals 25.4–33.3 ( $M=28.3$ )%.

Cheek depth is 18.2–27.8 ( $M=22.7$ )% head, and shows no obvious allometry with standard length.

Caudal peduncle length is 16.2–22.0 ( $M=19.0$ )% of standard length, and 1.3–1.9 (modal range 1.5–1.7) times its depth.

Mouth horizontal or almost so, the lips slightly but noticeably thickened, the jaws equal anteriorly. The posterior tip of the maxilla reaches a vertical closer to the anterior orbital margin than to the nostril, rarely extending to a vertical through the margin of the orbit.

Lower jaw 1.5–2.0 (mode 1.8) times longer than broad, its length 33.3–39.0 ( $M=36.0$ )% of head length. Ascending processes of the premaxilla 25.7–34.3 ( $M=30.6$ )% of head.

*Gill-rakers and pharynx.* There are 8–10 (mode 10), relatively short and moderately stout gill-rakers in the outer row on the lower part of the first arch; the lowermost one or two rakers are smaller than the others. The rakers are transversely elongate, with the upper surface produced into two or three cusp-like projections. Microbranchiospines are present.

In his original description of *Tilapia steindachneri* (see synonymy above), Boulenger (1913) gave the gill-raker count as 13–14, a count repeated in his redescription of 1915. These figures, however, apply only to those syntypes which Regan (1922) ultimately referred to *Sargochromis mellandi*. The remaining syntypes, which I refer to *Th. buysi*, have only 9 or 10 rakers.

The dorsal pharyngeal epithelium is thickened and thrown into well-defined, approximately longitudinal furrows, the crests of the ridges often further developed into low papillae. Immediately anterior to the toothed upper pharyngeal bones of each side, the buccal roof is produced into a prominent pad which, however, has neither the size nor the shape of the visor-like hanging pad found in certain cichlid genera (see Trewavas, 1974: 389–392, and Greenwood, 1983: 265–267).

*Scales* are ctenoid below the level of the lower lateral-line, cycloid above it and on the chest. The chest scales are small, except for a midventral row of slightly larger scales, and are noticeably smaller than those on the ventrolateral aspects of the flanks and on the belly. The size transition is abrupt and takes place along a line connecting the pectoral and pelvic fin insertions, or a little behind that line.

There are 32 (rare) to 36 (rare) scales, modally 34, in the lateral-line series,  $4\frac{1}{2}$ – $6\frac{1}{2}$  (modally 5 or  $5\frac{1}{2}$ ) between the dorsal fin origin and the upper lateral-line, and 7–9 (mode 8) between the pectoral and pelvic fin bases. Cheek with 3–5 (mode 4) scale rows, the scaled area with a clearly demarcated, naked embayment anteroventrally. Each of the last 3 or 4 pored scales in the upper lateral-line is separated from the dorsal fin base by one large and one small scale.

*Fins.* Dorsal with 14 (f1), 15 (f17), 16 (f26) or 17 (f2) spinous and 10 (f2), 11 (f24), 12 (f18) or 13 (f2) branched rays. Anal with 3 spinous and 7 (f8), 8 (f37) or 9 (f1) branched rays.

In all but three of the 46 specimens examined, small, almond-shaped sheath scales are present at the base of the anal fin (see p. 188 above). The horizontal extent of these varies from a row extending along the entire spinous part of the fin and reaching the 3rd–5th branched ray, to a few isolated and often non-imbriating scales at the base of either or both the spinous and the anterior part of the soft fin; sometimes only one or two scales are present and then usually at the base of the first one or two spines.

The pectoral fin length is 19.6–26.4 ( $M = 21.1$ )% of standard length, 61.3–80.0 ( $M = 70.2$ )% of head length. The pelvic fins have the first branched ray longer than the second, most noticeably so in adult males, but never produced into a filamentous extension, and never reaching to the origin of the anal fin.

The caudal fin generally is subtruncate, but is almost truncate in a few specimens; it is scaled on its proximal third to half.

*Teeth.* The *outer row* in both jaws of fishes up to *ca* 90 mm SL is composed, mostly, of relatively slender, unequally bicuspid and gently recurved teeth. The small minor cusp is angled away from the vertical axis of the major cusp (Fig. 2A). In teeth from the upper jaw, the tip of the major cusp usually lies within, or but slightly beyond, the vertical formed by the outer margin of the tooth; in lower jaw teeth, however, the tip often lies well outside that line, as it may occasionally do in upper jaw teeth as well.

Posteriorly in the premaxillary outer row of most specimens there are from 2 to 8 unicuspid teeth. These teeth, unlike those in *Astatotilapia* (see Greenwood, 1979), are not noticeably enlarged nor are they caniniform.

Although some unicuspid teeth are present laterally and anteriorly in the jaws of fishes less than 90 mm SL (especially those in the 75–90 mm range), their frequency only increases in specimens over 90 mm SL, becoming the predominant form in fishes more than 110 mm SL; even in these specimens, however, a few weakly bicuspid teeth are present in both jaws. The unicuspid teeth are slender and slightly recurved, and do not have the near-cylindrical neck and crown of typical caniniform teeth. Both uni- and bicuspid teeth often show pronounced wear at the tip of the crown.

There are 42–66 (modal range 50–62) teeth in the outer premaxillary series, the number not showing any clear-cut allometry with the fish's standard length.

*Inner series.* It is difficult to generalize about tooth form in these rows because there is both a change with growth and, apparently, some inter-population differences as well.

Most fishes less than 85 mm SL have a predominance of slender tricuspid teeth in the inner rows; the median cusp of these teeth is longer and broader-based than are the cusps flanking

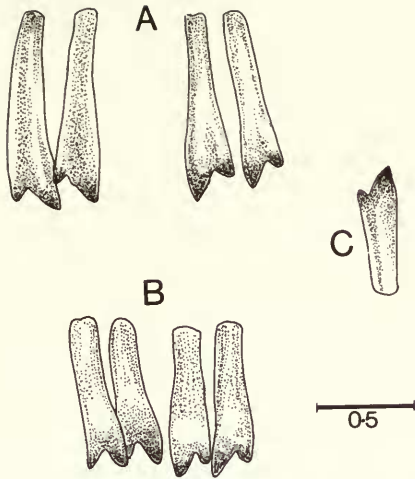


Fig. 2 Outer row jaw teeth of: A, *Thoracochromis buysi*; B, *Th. albolabris*; C, *Orthochromis machadoi*. A & B are anterior premaxillary teeth, C, a tooth from the anterior part of the dentary.

it. A few slender bicuspid and weakly bicuspid, nearly unicuspid teeth are interspersed amongst the tricuspids, especially in fishes over 70 mm SL. Such teeth become more frequent in specimens between 75 and 85 mm SL. In specimens from certain localities, however, this admixture of tricuspids, weakly tricuspid and bicuspid is found in much smaller fishes, even among individuals as small as 47 mm SL.

Fishes above *ca* 80 mm SL from all localities show a further increase in the number of bi- and unicuspid inner teeth, coupled with a decline in the number of tricuspids. These latter also tend to be less distinctly tricuspid, the median cusp gaining in dominance over the lateral ones. Specimens more than 90 mm SL have an essentially unicuspid inner dentition, although a few bicuspid and weakly bicuspid teeth persist; only the largest fish examined, 118.0 mm SL, has the inner rows composed solely of unicuspid.

Anteriorly and anterolaterally the inner teeth are arranged in 2 (mode) or 3 rows, rarely in a single irregular row. Posteriorly in both jaws, however, only a single row of teeth is present.

All but a few of the specimens examined have the dental mucosa greatly thickened with the result that just the tips of the teeth are visible. That this situation is a preservation artefact, cannot be overruled.

*Lower pharyngeal bone and dentition.* The lower pharyngeal bone has an approximately triangular and equilateral dentigerous surface; the anterior shaft is short (Fig. 7A). Except for about the posterior four or five teeth in the median tooth rows, the pharyngeal teeth are slender, compressed and cuspidate, and are closely spaced. The exceptional teeth are distinctly coarser and larger than their lateral congeners, but still retain a cuspidate crown. Sometimes a few posterior teeth in the rows immediately lateral to the median row are slightly coarser than the other lateral teeth.

The pharyngeal bone itself is not enlarged, and has slender posterior horns.

*Osteology. Neurocranium.* Overall skull morphology in this species (Fig. 10A) departs slightly from the generalized haplochromine type (Greenwood, 1979: 274) in being more slender, with a shallower and narrower otico-occipital region, narrower interorbital and ethmoid regions, and in having a lower and less expansive supraoccipital crest. Also the dorsal skull profile, from the anterior tip of the supraoccipital bone to the tip of the vomer, slopes less steeply (*ca* 30° compared with *ca* 45° in the case of *Astatotilapia nubila* or *A. bloyeti*; cf Fig. 10A with fig. 6 in Greenwood, 1979).

Expressed as percentages of neurocranial length, the orbital depth is 34.8–36.3%, pre-orbital depth 17.4–20.8%, preotic skull length 63.6–66.6%, ethmoverine length 27.0–27.4%,

depth of otic region 37.5–40.0%, width of otic region 50.0%, and greatest height of supra-occipital crest 16.5–18.2% (Data from three skulls, 22.0, 23.0 and 24.0 mm neurocranial length; for definition of measurements see Greenwood, 1980: 4–5).

The apophysis for the upper pharyngeal bones is of the *Haplochromis* type (Greenwood, 1978); in two of the three skulls examined the basioccipital contribution to the facet is large, but in the third it is greatly reduced.

*Suspensorium* (Fig. 3A). There is a distinct gap between the palatine and entopterygoid bones, an unusual features so far recorded only in members of the *Ophthalmotilapia* assemblage of Lake Tanganyika, and in at least some *Lethrinops* species (Lake Malawi); for a discussion of this feature see Greenwood (1983: 254–6, and 279).

The hyomandibula in *Th. buysi* (Fig. 3C) has a fairly well-developed anterior flange, but one which is less expansive than that in *Orthochromis machadoi* (see Fig. 3E).

*Jaws*. The *dentary* (Fig. 11A) is a slender bone, with its alveolar surface flared outwards so as to form a shelf-like overhang above the bone's lateral face. There is no mental projection in the symphyseal region, which is, however, a little swollen.

The *premaxilla* (Fig. 8A) has no outstanding features. Its ascending processes are long (almost one fifth longer than the dentigerous arm) and have a slight but obvious posterior

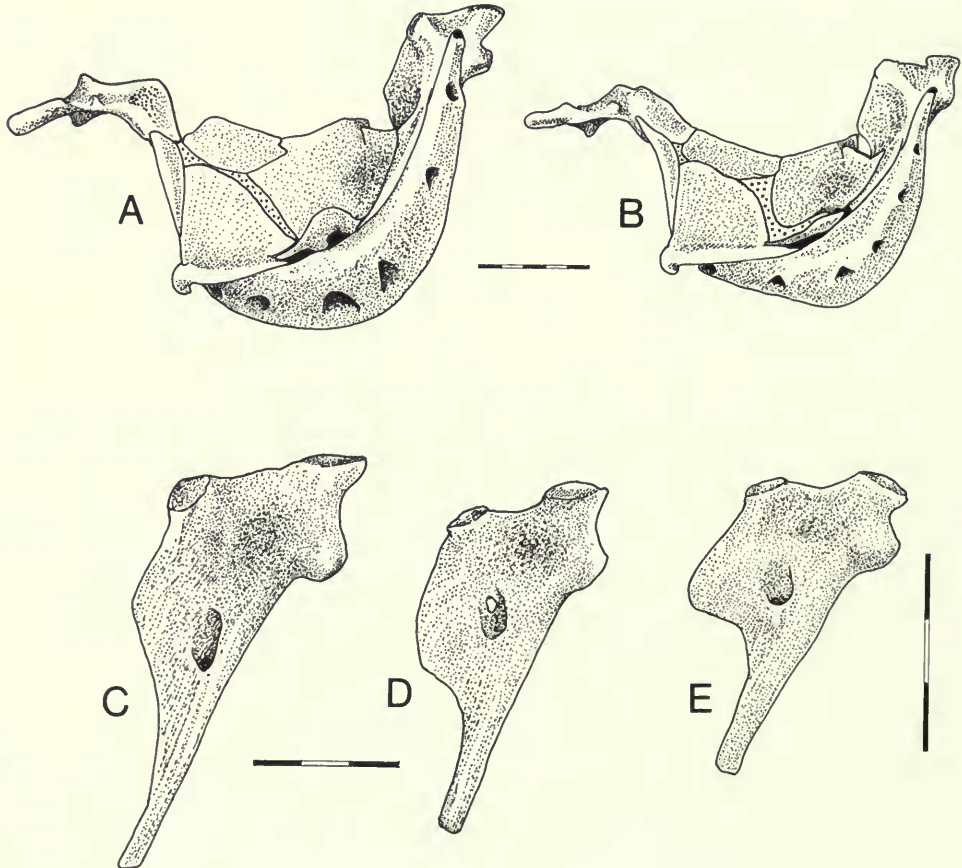


Fig. 3 A, Suspensorium of *Thoracochromis buysi*; B, that of *Th. albolabris*, both in left lateral view. C, D & E, hyomandibula, in left lateral view, of C, *Th. buysi*; D, *Th. albolabris*; E, *Orthochromis machadoi*. Scale in mm.



inclination at an angle of about 10° from the vertical. The dentigerous arms are laterally compressed and are not expanded anteriorly and anteroventrally to form a beak-like process.

*Caudal fin skeleton.* All the hypurals are free in 22 of the specimens radiographed but in some hypurals 3 and 4 are very closely apposed to one another, and in two others hypurals 1 and 2 are fused. In another fish, hypurals 1 and 2 seemingly are fused distally but are free proximally, as are hypurals 3 and 4. All these observations were made from radiographs thus rendering it difficult to distinguish with certainty between actual fusion and close apposition.

*Vertebrae.* Excluding the fused  $PU_1 + U_1$  centra, there are 30 (f8), 31 (f10), 32 (f4) or 33 (f1) vertebrae, comprising 13 (f2) or 14 (f21) abdominal and 16 (f7), 17 (f10), 18 (f5) or 19 (f1) caudal elements.

The syntypical specimens of *Tilapia steindachneri*, from the Que river, are excluded from these counts; here the range is 28 (f1), 29 (f1) and 31 (f3), comprising 12 (f1), 13 (f1) or 14 (f3) abdominal, and 15 (f1) or 17 (f4) caudal centra.

In her original description of *Th. buysi*, Penrith (1970: 169) gives the vertebral count (including  $PU_1 + U_1$ ) for the holotype as 16 + 18; I have checked this figure on a radiograph made in the BM(NH), and find that my count, including the  $PU_1 + U_1$  elements, is 14 + 18.

*Coloration.* No information is available on live colours. For material fixed in formol and preserved in alcohol, the coloration is: *Females and immature males*, with a light brown (beige) ground colour which often becomes silvery on the belly and the flanks below the midlateral line. The intensity and presence of the silvery pigment may depend on factors of preservation since in some specimens it is absent, the beige colour merely lightening on the lower half of the belly. In those specimens which are silvery, faint traces of silver are present on the cheek and, more intensely, on the operculum. Traces of from 8–12 vertical bars are visible on the flanks and caudal peduncle; some of these bars extend almost to the ventral body profile, but most fade and disappear slightly below the level of the midlateral line. The intensity and clarity of the bars is very variable in the sample as a whole, but are reasonably constant within any one sample. Dr Michael Penrith (*in litt*) has observed, for the small cichlids of the Cunene, that coloration is generally darkest in fishes from the upper reaches of the river.

All fins are greyish-hyaline, the *dorsal* with darker pigmentation between the spines, and dark maculae between the branched rays; the lappets are darker than the areas between the spines. The *caudal* fin is faintly maculate, with a dark posterior margin; this marginal band is most obvious when the fin is closed. The *anal* has dark lappets, and some indication of a dark margin to the anterior region of the soft part as well. In some males there are 5 or 6 dark spots, arranged, somewhat irregularly, in two rows on the soft part of the fin; the distal row lies a little above the fin's margin, the proximal row (usually with fewer spots) lies along the middle of the fin. There is no indication of a clear surround encompassing each of the spots, which thus cannot be considered true ocelli. The *pelvic* fins sometimes have a peppering of dark chromatophores which are most obvious in males.

*Sexually active males.* In the few sexually active males examined, the overall coloration is much darker than that in females and inactive males. Scales above the midlateral line are outlined in dark brown, the vertical barring is moderately intense, the dorsum of the head and the entire snout is dark, almost dusky, as are the rami of the lower jaw and the anterior two-thirds of the lower lip. The branchiostegal membrane and the chest are dusky, but are lighter than the dentaries. The cheek is brown and only a little darker than the ground colour of the body.

The membrane between the *dorsal fin* spines is almost black, but the lappets are hyaline; the soft part of the fin is densely maculate, the spots having a clear centre and a narrow, very dark brown surround. The proximal two-thirds of the *caudal fin* is covered in similar maculae, but its distal third is a somewhat dusky hyaline; the posterior margin is dark. The *anal fin* has a dusky hyaline ground colour showing between the large number, 8–10, of pale spots, each with a narrow, dark surround. The spots are arranged in three irregular rows (with from one to three spots in each) on the soft part of the fin. The anal spots are about

four times larger than the biggest maculae occurring posteriorly on the dorsal fin. The *pelvic fins* are very dusky, almost black over the proximal half of each fin. The *pectorals* are hyaline.

**DISTRIBUTION.** *Thoracochromis buysi* is known only from the Cunene river, including one of its tributaries, the Que.

**DIAGNOSIS AND AFFINITIES.** Within the genus *Thoracochromis*, this species would seem, at least anatomically, to be a relatively primitive member of the group. This is particularly so when comparisons are made with species from the Nile and Lake Turkana (see Greenwood, 1979: 293–4). Unfortunately, insufficient information is available for many species occurring in Lake Mweru and the Zaire system to indicate what level of relationship might exist between them and *Th. buysi*. What information we have, however, does not suggest that a sister-species relationship is likely.

In their overall appearance and most anatomical characters, two of the other Angolan *Thoracochromis* species, *Th. schwetzi* and *Th. lucullae*, are very similar to *Th. buysi*. Neither species occurs in the Cunene river, and only *Th. schwetzi* is well-represented by numerous specimens.

*Thoracochromis buysi* differs from *Th. lucullae* mainly in having the depth of the pre-orbital bone greater, and not less than, the interorbital width (or, rarely, equal to it), and in details of its dentition. In *Th. lucullae*, the outer row jaw teeth have a relatively larger and broader minor cusp, with the result that its teeth are less unequally bicuspid than are those in *Th. buysi*. There are indications from the few available specimens of *Th. lucullae* that the scales are larger than in *Th. buysi*; there are 32 lateral-line scales in *Th. lucullae* as compared with a modal count of 34 or 35, rarely 32 or 36, in *Th. buysi*, and the cheek scale rows are generally more numerous in *Th. buysi* (3–5, mode 4, cf 3 in *Th. lucullae*). Neurocranial form, and the osteological features of the jaws, are similar in the two species, although the narrower interorbital region in the skull of *Th. buysi* is very obvious. The suspensorium is damaged in the only skeleton of *Th. lucullae*, so it is impossible to check whether or not that species has a palatopterygoid gap (see p. 194 above).

*Thoracochromis buysi* is also very similar to *Th. schwetzi*, which differs, however, in having unicuspid jaw teeth in specimens of a much smaller size. It also differs in generally having only a single series of inner teeth anterolaterally in both jaws, compared with the modal condition of 2 or 3 rows in *Th. buysi*. Like *Th. lucullae*, *Th. schwetzi* has a shallower preorbital bone than *Th. buysi* (15.8–20.0% head length, cf 18.5–26.0, M=22.9% in *Th. buysi*) the depth of which is always less than the least interorbital width.

In all three species the basic shape of the bicuspid outer row jaw teeth is similar, as is that of the tricuspid inner teeth. The unicuspid outer teeth in *Th. schwetzi*, however, are more slender and cylindrical in cross-section than are the unicuspid teeth occurring in the other two species.

The overall similarity of these three species, each from a different river system, might suggest that each is the vicariant (*i.e.* replacement) sister-species of the others. However, it must be stressed that there are as yet no synapomorphic characters known to be uniquely shared by the three taxa, and so their possible sister-species relationship cannot be established unequivocally.

*Thoracochromis buysi* differs from *Th. albolabris*, the fourth Angolan member of the genus, in several characters, all of which are autapomorphic for *Th. albolabris*. The most obvious of these are the greatly thickened, often lobate lips of *Th. albolabris*, the very small chest scales in that species, and its narrower, near V-shaped dental arcades (see p. 201).

Regrettably, I have not been able to examine the holotype of Steindachner's species '*acuticeps*', whose generic status thus remains unknown. It is clear from Penrith's (1970: 171) comments, and from Dr Trewavas' personal examination of the *acuticeps* type specimen, that *Th. buysi* differs from it in several features. In particular, *Th. buysi* has a less massive lower pharyngeal bone with smaller median pharyngeal teeth, and its lower jaw is shorter than in '*acuticeps*'.

The precise locality from which the type of '*acuticeps*' was collected is unknown, and no descriptions of additional material have ever been published, apart, that is, from Regan's (1922) account which is clearly based on a polyspecific sample (see Trewavas, 1973: 31, and personal observations).

### Study material and distribution records

#### Registered material

Museum register number	Locality
Staatsmuseum Windhoek 5099 (Holotype)	Cunene river mouth
SAM 25243 (paratype)	Cunene river mouth
BMNH; P=collection number:	
1984.2.6:1-7 P1682	Cunene R., Ondurusu falls (17° 24' S, 13° 56' E).
1984.2.6:8 P1347	Cunene R., Ondurusu falls (17° 24' S, 13° 56' E).
1984.2.6:9-14 P1403	Cunene R., Ondurusu falls (17° 24' S, 13° 56' E).
1984.2.6:15-18 P1422	Cunene R., Ondurusu falls (17° 24' S, 13° 56' E).
1984.2.6:19-23 P589	Cunene R., below Ruacana falls (17° 24' S, 14° 13' E).
1984.2.6:24 P89	
1984.2.6:25-27 P121	Cunene R., 3 miles west of Swartbooisdrif. (17° 19' S, 16° 58' E).
1984.2.6:28-38 P1780	Foz do Cunene (17° 15' S, 11° 43' E).
1984.2.6:39-52 P1781	Foz do Cunene (17° 15' S, 11° 43' E).
1984.2.6:53 P1841	Cunene R., Otjinungwa (17° 12' S, 12° 20' E).
1984.2.6:54 P1126	Cunene R., Matala Dam, Luceque (14° 36' S, 15° 18' E).
1984.2.6:55-56 P1128	Cunene R., Matala Dam, Luceque (14° 36' S, 15° 18' E).
1984.2.6:57-62 P1157	Cunene R., Chitapua (14° 23' S, 15° 18' E).
1984.2.6:63 P1186	Cunene R., Jamba-ia-Homa (13° 46' S, 15° 30' E).

#### Unregistered material

Locality	Number of specimens	Collection no.
Cunene R., 10 miles west of Ruacana (17° 26' S, 14° 05' E).	2	P611
Cunene R., Ondurusu falls (17° 24' S, 13° 56' E).	1	P1416
Cunene R., Ondurusu falls (17° 24' S, 13° 56' E).	4	P1347
Foz do Cunene (17° 15' S, 11° 43' E).	10	—
Cunene R., Otjinungwa (17° 12' S, 12° 20' E).	1	P1324
Cunene R., Otjinungwa (17° 12' S, 12° 20' E).	1	P1325
Cunene R., above Epupa falls (17° 00' S, 13° 15' E)	1	P696
Cunene R., near Cafu (16° 30' S, 15° 10' E).	1	P808
Cunene R., 82 km west of Ondurusu falls (15° 59' S, 13° 22' E).	5	P1289
Cunene R., Chitapu (14° 23' S, 15° 18' E).	3	P1116
Cunene R., Chitapu (14° 23' S, 15° 18' E).	1	P1176

#### *Thoracochromis albolabris* (Trewavas & Thys van den Audenaerde), 1969

SYNONYMY. *Haplochromis albolabris* Trewavas & Thys van den Audenaerde, 1969. *Mitt. zool. St. Inst. Hamb.* 66: 237-239, figs 1 & 2, plate 13.

DESCRIPTION. Based on 18 specimens, *ca* 30-121.0 mm SL. Since 11 of these specimens

were badly distorted before or during preservation, morphometric features are taken from 7 individuals only, 37.0–121.0 mm SL; these include the holo- and paratype of the species. Information on dentition, lip form and various meristic characters are, however, supplemented by data taken from the distorted specimens. Because the sample size from which the morphometric characters are derived is so small, ranges but not means or modes are given for those features.

Depth of body 29.7–34.5% of standard length, length of head 32.0–36.7%.

Dorsal head profile straight or very gently curved, sloping at an angle of 30°–35° to the horizontal, its outline sometimes interrupted by the slight prominence of the premaxillary ascending processes. The upper margin of the orbit lies distinctly below the outline of the head.

Preorbital depth 16.0–22.4% of head length, least interorbital width 16.0–21.4%. Preorbital depth and interorbital width are equal in 2 specimens, the preorbital depth is greater in 4 others, and the interorbital width is greater in one specimen (see p. 191 above).

Snout length 36.0–44.0% of head length and 1.3–1.6 times its breadth; in one exceptional specimen the length-breadth ratio is 1.9.

Eye diameter 25.0–32.0% of head length, the largest eye being that in the smallest specimen measured (37.0 mm SL). Cheek depth is 19.6–24.2% of head length.

The caudal peduncle is 1.3–1.7 times longer than deep, its length 17.0–19.3% of standard length.

With such a small sample it is impossible to detect any features which might vary allometrically with standard length. The highest percentage ratios for preorbital depth, interorbital width, and pectoral fin length (see below) are, however, those for the smallest individual measured.

The lips exhibit a wide but continuous variation in form, from those (as in the type specimens) which are clearly much thickened, but uniformly so (Fig. 4), those which are not only thickened but are produced medially into prominent lobes (Fig. 5). This latter condition is identical with that occurring in extreme individuals of *Lobochilotes labiatus* (Lake Tanganyika) and *Paralabidochromis chilotes* (Lake Victoria) and in the one *Melanochromis labrosus* (Lake Malawi) available for study. The intermediate stages of lip development seen in *Th. albolabris* are also encountered in the first two species listed above; *M. labrosus* is known from too few specimens to allow comment on that point.

The degree of lip development in *Th. albolabris*, at least with respect to lobe formation, is not obviously size correlated; uniformly and distinctly thickened lips are present in

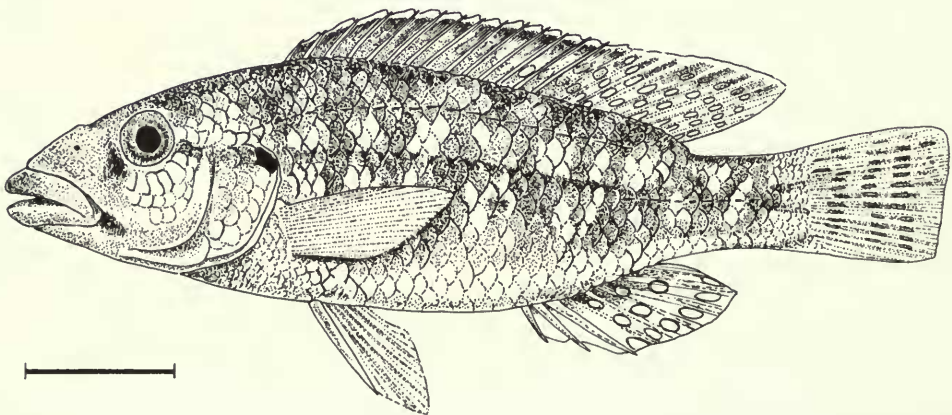


Fig. 4 *Thoracochromis albolabris*; after Trewavas & Thys van den Audenaerde (1969). Drawn by G. J. Howes. Scale = 20 mm.

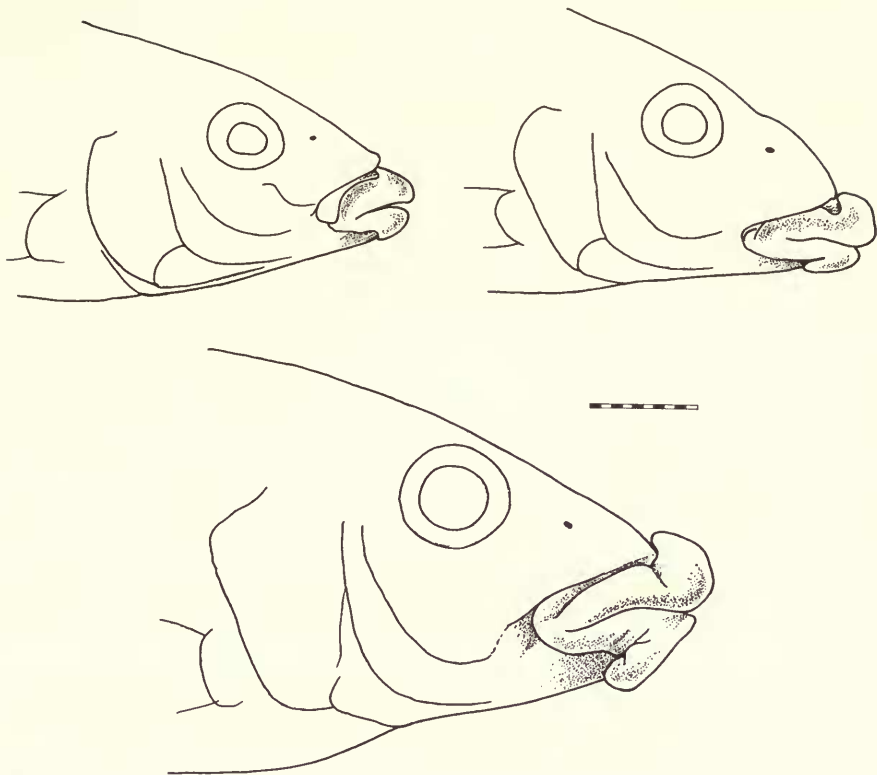


Fig. 5 *Thoracochromis albolabris*. Variations in lip and lobe development. Scale in mm.

specimens throughout the size range available. Some large specimens, for example the holotype 96 mm SL and the paratype 121 mm SL, have unlobed lips; incipient lobes are present in some specimens 33–76 mm SL, and moderate lobes are developed in a fish 77 mm long. Other individuals in the size range 30–40 mm show no trace of lobes, but the lips are developed to an extent comparable with those in the much larger type specimens. Fully developed lobes are found in fishes of 73, 92, 93 and 121 mm SL.

Because some large specimens lack lobes it is impossible to determine whether or not small specimens without lobes are at an early stage of future lobe development. But, judging from the sample studied it seems probable that lobes are not well-developed in fishes of less than 45–50 mm standard length.

Since considerable variation in the extent of lobe development is recorded for other cichlid species (see Greenwood, 1981 for the Lake Victoria species), I have no doubt that this sample of *Cunene* fishes is conspecific, particularly since all share other, and uniquely derived features as well.

The mouth is horizontal or nearly so, the posterior tip of the maxilla either reaching a vertical passing close to the anterior orbital margin, or one lying about midway between it and the nostril.

The ascending processes of the premaxilla are 34.5–41.0% of head length, the length of the lower jaw 35.2–40.0% and its length-breadth ratio is 1.3–1.7.

*Gill-rakers and pharynx.* There are 11 (f1), 12 (f3), 13 (f3), 14 (f3), 15 (f4) or 17 (f1) rakers in the outer row on the lower part of the first gill-arch; one specimen has 9 rakers on one side and 11 on the other. Except for the lower 4 or 5 elements, the rakers are short and stout to moderately stout, transversely elongate, and with the upper surface generally thrown

into 2 or 3 cusps. The lower 4 or 5 rakers are reduced to little more than low knobs; the size-range of the lower rakers is positively correlated with the length of the fish, being barely visible in specimens less than 35 mm SL.

The microbranchiospines are sometimes difficult to detect, but although small are always present.

As in *Th. buysi*, the dorsal epithelium of the pharynx is thickened, noticeably corrugated and papillose. The prepharyngeal pads are well-developed and are like those of *Th. buysi* in size and shape.

*Scales* are weakly ctenoid on the flanks below the upper lateral-line, and are very weakly ctenoid to cycloid on the caudal peduncle and above the upper lateral-line on the flanks. In larger specimens the degree of ctenoidy is weaker than in smaller individuals.

The size-transition between the scales on the chest and those on the ventrolateral aspects of the flanks is abrupt; the chest scales are very small and deeply embedded. Two specimens appear to have small naked areas ventrolaterally on the chest, but closer examination shows that the scales in these areas are more deeply embedded than elsewhere in the region.

There are 32 (f1), 33 (f7), 34 (f5) or 35 (f3) scales in the lateral-line series,  $4\frac{1}{2}$  to  $6\frac{1}{2}$  (generally 5 or  $5\frac{1}{2}$ ) between the dorsal fin origin and the upper lateral-line, and 8 to 10 between the pectoral and pelvic fin insertions. The cheek has 3 to 5 scale rows (usually 3), generally embedded deeply in the thickened skin. Anteroventrally there is a distinct but sometimes small naked embayment, and there is always a narrow naked strip between the cheek scales and the preoperculum.

With one exception, all specimens have one large and one small scale between each of the last 4 or 5 scales in the upper lateral-line and the dorsal fin base. In the exceptional fish there are, on one side, two large scales between the lateral-line and the fin, and on the other side two large and one small scale.

*Fins.* Dorsal with 14 (f1), 15 (f14) or 16 (f1) spinous and 10 (f2), 11 (f9) or 12 (f5) branched rays, the anal with 3 spinous and 7 (f4), 8 (f10) or 9 (f1) branched elements.

All but three fishes (30–35 mm SL) have either a well-developed scale sheath at the base of the anal, or isolated sheath scales present in that region, even in specimens as small as 33–34 mm SL.

The pectoral fin is 18.9–25.0% standard length, 56.0–66.8% of head length. The pelvic fins have the first branched ray only a little longer than the second, or rarely, the two are of equal length. In large adult males, however, the first ray is clearly longer than the second, but is not drawn out into a distally filamentous projection.

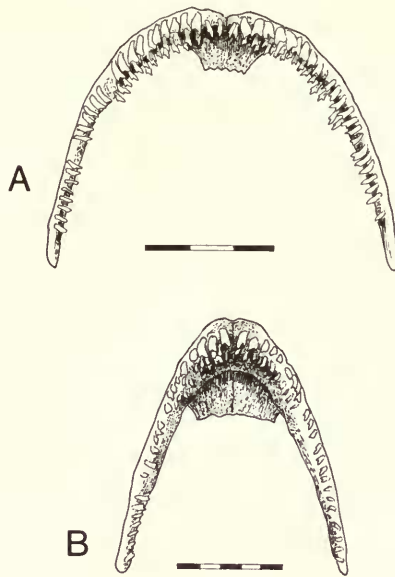
The caudal fin is subtruncate and is scaled over its proximal third to half, or exceptionally, over its proximal two-thirds.

*Teeth.* The dental arcade in *Th. albolabris* (Fig. 6) is more nearly 'V'- than 'U' shaped, especially in specimens with fully lobate lips. A similar correlation of arcade shape with lip development is seen in other species, mentioned above, with lobed lips (Greenwood, 1959: 209, and other observations).

The *outer teeth* (Fig. 2B), in virtually all the specimens have worn cusps, thus making it difficult to describe accurately the form of the crown. Unworn teeth in fishes over 75 mm SL are either unicuspid or weakly bicuspid; in bicuspids the minor cusp, although reduced as compared with that cusp in *Th. buysi*, does show a similar angling away from the major cusp. Fishes in this size range generally have unicuspid teeth posteriorly in the premaxillary series. As in *Th. buysi*, these and other unicuspids are slender and relatively compressed, with attenuated rather than pointed crowns; that is, they could not be described as caniniform.

From the sample available it seems that in fishes less than 75 mm SL the majority of unworn teeth are distinctly but unequally bicuspid, with a cusp shape and arrangement like that in the weakly bicuspid teeth of larger individuals. Teeth situated posteriorly in the outer premaxillary row of these smaller fishes are weakly bicuspid.

There are 22–64 teeth in the outer premaxillary series, the number probably having a positive correlation with standard length, although in one of the largest specimens (121 mm SL) there are only 50 teeth, and a specimen of 37 mm has 60.



**Fig. 6** Premaxilla, in occlusal view, of: A, *Thoracochromis buysi*; B, *Th. albolabris* to show difference in outline of dental arcade; only the basal region of the ascending processes is shown. Scales in mm.

The *inner teeth* are arranged, anteriorly and laterally, in from 1 to 4, usually 2, rows in the upper jaw, and in 1 to 3, usually 2, in the lower jaw; posterolaterally in both jaws only a single row is present.

Fishes less than 70 mm SL have mostly weakly tricuspid inner teeth in which the larger median cusp is flanked by slight, shoulder-like projections. Fishes over 70 mm SL may have an admixture of tri- and weakly bicuspid teeth or of bi- and, predominantly, weakly bicuspid, or most of the teeth may be unicuspid.

*Lower pharyngeal bone and dentition* (Fig. 7B). The anterior shaft is short, the dentigerous area triangular and varying from slightly longer than broad, through equilateral, to slightly broader than long. Some variation exists in the stoutness of the bone. In the holotype it is moderately stout, the stoutest seen amongst the specimens available. In other, and larger, fishes the bone is but slightly thickened, while in the majority of specimens it shows no marked departure from the generalized condition seen in *Th. buysi*.

There is variation, too, in the degree to which teeth in the median pair of tooth rows are enlarged or coarsened. Certain of the larger specimens (including the holotype) have some of these teeth distinctly enlarged with near-molariform crowns, but in the majority of specimens the teeth are slender and cuspidate, those situated in the posterolateral corners of the dental field being more closely spaced than elsewhere.

*Osteology.* The *neurocranium* is similar to that of *Th. buysi* (Fig. 10B) in its general form, but has a lower supraoccipital crest, a flatter (that is, less concave) interorbital skull roof, and a convex not concave surface to the posterior part of the roof contributed by the frontals. The apophysis for the upper pharyngeal bones is of the *Haplochromis* type, but in some specimens the basioccipital contribution to the facet is rather small (although never as small as in the *Tropheus* type of apophysis; see Greenwood, 1978).

Expressed as percentages of neurocranial length (18.5 mm in the one skull available for measurement) the orbital depth is 37.9%, the preorbital depth 23.3%, the ethmovomerine

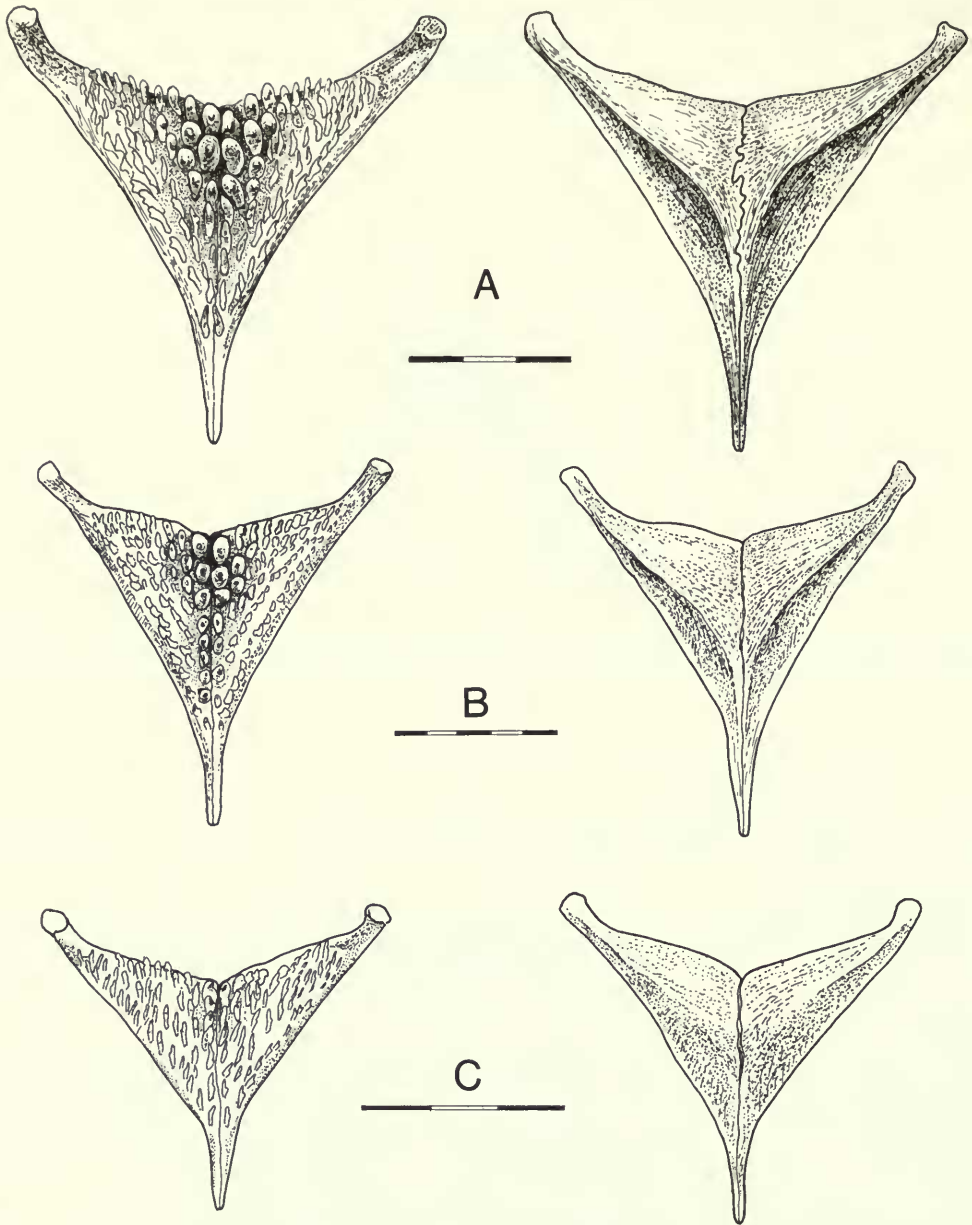


Fig. 7 Lower pharyngeal bones, in occlusal and ventral views, of: A, *Thoracochromis buysi*; B, *Th. albolabris*; C, *Orthochromis machadoi*. Scale in mm.

length 28.7%, the depth of the otic region 39.9%, the width of the otic region 51.3%, and the greatest height of the supraoccipital crest 13.5%.

*Suspensorium.* Unlike that in *Th. buysi*, the suspensorium in *Th. albolabris* (Fig. 3B) has no gap between the palatine and entopterygoid bones, and the posterior margin of the palatine is gently curved rather than rectangular. The anterior flange on the hyomandibula in *Th. albolabris* is slightly more expansive than in *Th. buysi*.

*Jaws.* Relative to that in *Th. buysi*, the maxilla in *Th. albolabris* is foreshortened (Fig. 8D & E). The *premaxilla* (Fig. 8B) has elongate ascending processes which are about 1.25



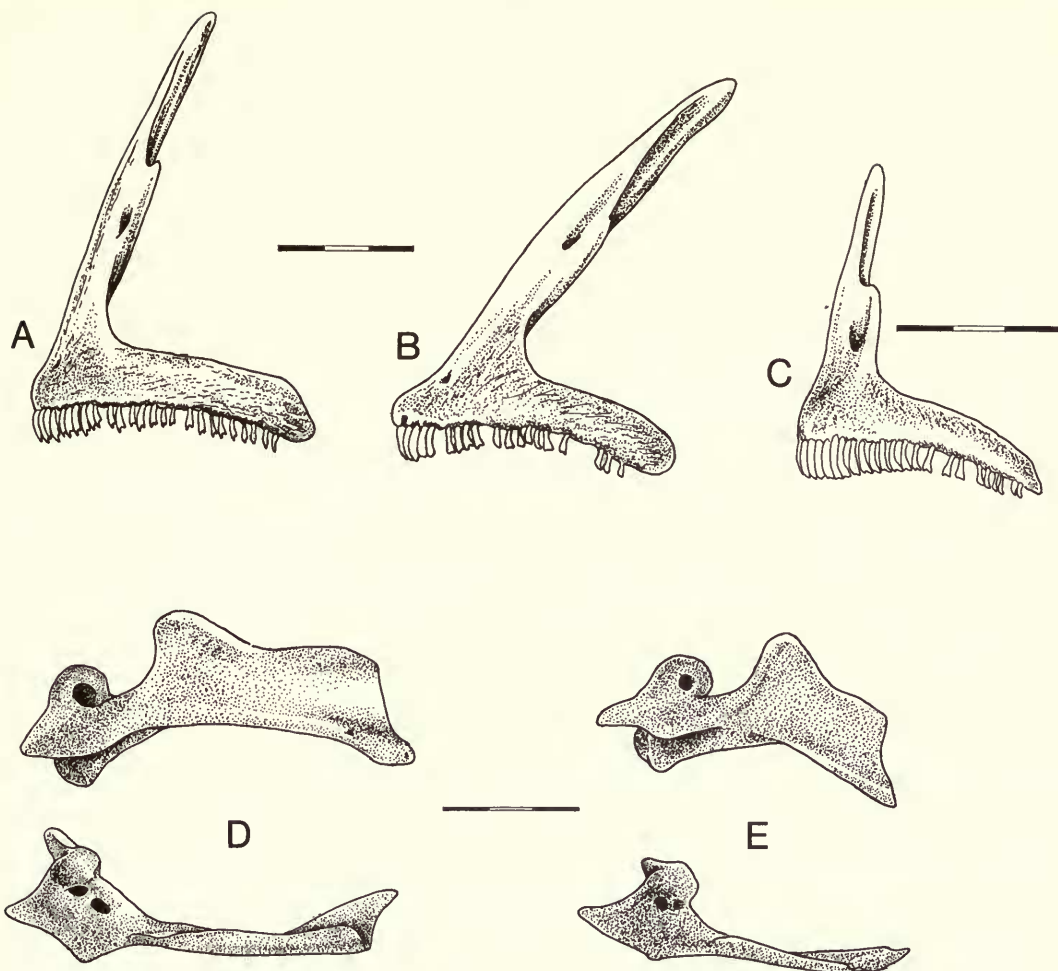


Fig. 8 Premaxilla (upper row) of: A, *Thoracochromis buysi*; B, *Th. albolabris*; C, *Orthochromis machadoi*. Maxilla, in left lateral and dorsal view (middle and lower rows respectively) of: D, *Th. buysi*; E, *Th. albolabris*. Scale in mm.

times the length of the dentigerous arms, and which slope strongly backwards at an angle of about  $25^\circ$  to the vertical. In occlusal view the two dentigerous arms are arranged so as to form a 'V'-rather than a 'U'-shaped outline (Fig. 6). These arms are not inflated, but anteriorly and somewhat anteroventrally each is produced forward beyond the base of the ascending process to form a prominent, shelf-like beak (Fig. 8B). The dentary (Fig. 11B) is like that in *Th. buysi*, but the rami of each side meet to form a more nearly 'V'-shaped occlusal surface in *Th. albolabris*, and the anterior 'shelf' is more prominent.

**Caudal fin skeleton.** All five hypurals are separate from one another in six of the nine specimens examined (1 alizarin specimen and 8 radiographs), but in the three others, hypurals 3 and 4 are so closely apposed as to appear almost fused.

**Vertebrae.** Excluding the fused  $PU_1$  and  $U_1$  centra, there are 30 (f2) or 31 (f5) vertebrae, comprising 13 (f1) or 14 (f6) abdominal and 16 (f2), 17 (4) or 18 (f1) caudal elements.

**Coloration.** Live colours are unknown, and the coloration can only be described for formol fixed and alcohol preserved specimens.

There are no sexually active fishes in the entire sample available for study. *Immature and sexually quiescent individuals of both sexes* have a similar coloration. The ground colour is light brown (beige), darkening to greyish-beige on the dorsum of the head in some individuals. The body is crossed by 7–10 bars, often of irregular outline and shape, and either vertically or somewhat obliquely aligned. Some may be simple bars, others are narrowly triangular with, in any one specimen, the apex directed either dorsally or ventrally. Several specimens have a faint and narrow midlateral stripe extending the whole length of the body; a second narrow band runs along the upper lateral-line scale row, interconnecting the bars over the posterior half of the body. In some specimens there is a rather broad but faint lachrymal stripe running from the anteroventral margin of the orbit to the angle of the jaw; others have, in addition, a narrow bar across the snout between the anterodorsal margins of the orbits.

All the fins are hyaline, the spinous *dorsal* with dark streaks between the rays, and dark lappets; the soft dorsal is fairly densely maculate, the maculae either solid, or light-centred with a ring of dark marginal spots circumferentially. The *caudal* is densely and darkly maculate over most of its length, with, in at least some individuals, a dark posterior margin. In one of the males examined there are numerous light-centered but dark margined spots arranged rather irregularly in two or three rows; none of the spots has a clear surround. Other males, and most females, have the anal fin hyaline, but in some almost the anterior half of the anal fin is a light greyish-sooty colour. The *pectoral* and *pelvic* fins are hyaline, but in one male there are faint dusky areas over about the anterior third of the pelvic fins.

The figure of the holotype, a male, published by Trewavas and Thys van den Audenaerde (1969: plate 1) gives a good impression of a darkly pigmented fish; the specimen, however, is now somewhat faded.

**DISTRIBUTION.** Known only from the Cunene river, see also p. 205.

**DIAGNOSIS AND AFFINITIES.** Specimens of *Th. albolabris* with lobed lips are immediately distinguishable from all other cichlids occurring in the Cunene river. Those specimens without obvious lobes are recognisable by the degree to which the lips are thickened and by the near 'V'-shaped dental arcade, both features which, of course, also serve to diagnose lobe-lipped individuals as well.

*Thoracochromis albolabris* is further distinguished from all Cunene haplochromines, except *Orthochromis machadoi* (see p. 206), by the very small size of its chest scales, and from all, except the species of *Serranochromis*, by its high gill-raker counts (11–17). From the *Serranochromis* species it is distinguished by various dental characters and several morphometric features as well.

From *Orthochromis machadoi*, *Th. albolabris* is distinguished by its head shape, dental pattern, absence of naked areas on the chest, and by having the first branched pelvic ray at least equal in length to the second ray, and generally a little longer than it.

When first describing *Th. albolabris*, Trewavas and Thys van den Audenaerde (1969) compared the taxon with a then undescribed haplochromine which they considered to be '... very close to our species'. The undescribed species was *Th. buyisi*, from which *Th. albolabris* can be separated readily on the several features noted above, particularly the high gill-raker count. The two taxa do share certain features, for example, a similar tooth morphology and various meristic and morphometric similarities, but none can be considered as synapomorphies indicative of a sister-species relationship between these species. Indeed, the resemblances are all in plesiomorph characters.

When compared with the *Thoracochromis* species occurring in other parts of Africa (Greenwood, 1979), *Th. albolabris* does exhibit a large number of derived features, for example, the hypertrophy of its lips, the high gill-raker count, the beaked premaxilla with its strongly angled ascending process, and the near 'V'-shaped dental arcade. Again, none of these features is an intrageneric synapomorphy; as autapomorphies, none can be used to

## Study material and distribution records

Museum register number	Locality
ZMH 1784 (Holotype)	Cunene R., Matala (14° 43' S, 15° 04' E)
Stockholm Museum, NRM NNN/951989, 7151	Southern Angola; locality unknown. Collected by M. Fröhlich.
BMNH; P=collection no.	
1972.9.27:89	Cunene R., above Epupa falls (17° 00' S, 13° 15' E).
1984.2.6:101 P710	Cunene R., 1 mile east of Epupa falls (17° 00' S, 13° 15' E).
1984.2.6:87-89 P1483	Cunene R., Ondurusu falls (17° 24' S, 13° 56' E).
1984.2.6:90 P609	Cunene R., Ondurusu falls (17° 24' S, 13° 56' E).
1984.2.6:91 P1276	Cunene R., 32 km west of Ondurusu falls (17° 15' S, 13° 42' E).
1984.2.6:92-98 P1389 (one an alizarin prep.)	Cunene R., 54 km west of Ondurusu falls.
1984.2.26:99-100 P643 (one used for skeletal prep.)	Cunene R., 27 miles west of Ondurusu falls (17° 10' S, 13° 33' E).

establish the intrageneric relationships of *Th. albolabris*. That *Th. albolabris* shows such a high number of derived features would seem to negate the views of Trewavas and Thys van den Audenaerde (1969: 238), who considered that it should be ranked amongst the generalised haplochromines. For the moment, *Th. albolabris* must remain a phylogenetic isolate amongst its congeners.

In the hyperdevelopment of its lips, and in other, possibly correlated characters, *Thoracochromis albolabris* resembles *Paralabidochromis chilotes* of Lake Victoria, *Cyrtocara loboichilus* and *C. euchilus* (Lake Malawi), *Melanochromis labrosus* (Lake Malawi) and *Loboichilotes labiatus* (Lake Tanganyika). In each of these lakes there are other species, too, some still undescribed, which resemble *Th. albolabris* in having hypertrophied lips as well as sharing certain dental and osteological features with that taxon.

I have made detailed comparisons of *Th. albolabris* with all these species, and find that on the basis of various characters and character combinations, arguments can be deduced which would militate against postulating *Th. albolabris* as having a close phylogenetic relationship with any but one of them, namely *Melanochromis labrosus*. For example, the dentition and the morphology of the jaws, together with details of the neurocranial osteology in *Loboichilotes labiatus*, *Cyrtocara euchilus* and *Paralabidochromis chilotes* differ quite trenchantly from the condition seen in *Th. albolabris*, and in the two latter species there are differences in squamation patterns as well. Few anatomical details could be studied in *Cyrtocara euchilus*, a species represented in the BMNH collections only by the type specimen. It differs from *Th. albolabris* in having an *Astatotilapia*-type of chest squamation (see Greenwood, 1979: 270; fig. 1), and there also appear to be differences in the dental morphology of the two species.

On the basis of their sharing the greatest number of derived features, the Malawian *Melanochromis labrosus* would thus seem to be the species most closely related to *Th. albolabris*. Unfortunately, as *M. labrosus* is known only from one specimen, its osteology could not be studied in any detail. For that and other reasons, especially our great ignorance of cichlid interrelationships in general, I would not develop any further the suggestion that *Thoracochromis* and *Melanochromis labrosus* might be closely related.

*ORTHOCHROMIS* Greenwood, 1954

This genus, originally defined on the basis of one species, *Orthochromis malagaraziensis* (David), was later expanded to include three other taxa (see Greenwood, 1979: 295–7). At that time the Cunene river species, *O. machadoi* (Poll), was known only from the two types and one other specimen.

The greatly increased number of *O. machadoi* specimens now available for study requires that two of the diagnostic features for the genus be modified. In my 1979 paper (page 296) it was indicated that all the upper lateral-line pore-bearing scales in *Orthochromis* are each separated from the dorsal fin base by not more than one large and one much smaller scale. (The few anterior scales in the upwardly curving portion of the lateral-line are excluded from that generalization.) In *O. machadoi*, however, only the last 9–12 pored scales of the upper lateral-line are separated from the fin in this way, the more anterior scales having two large scales between them and the fin base; in one specimen only the last 3–5 scales have less than two equal-sized scales in that position. Apart from this exceptional specimen the number of lateral-line scales separated from the dorsal fin by less than two scales in *Orthochromis machadoi* is still high as compared with the usual condition in haplochromine genera, and represents a situation otherwise only found in *Ctenochromis* (see Greenwood, 1979: 287). Even here the modal number of lateral-line scales involved (8 or 9) is lower than in *O. machadoi*.

Although *O. machadoi* can be described as having a relatively elongate and slender body (see Greenwood, 1979: 296) its body depth is now known to range as high as 34.5% of standard length (*cf* the maximum of 30% cited in Greenwood, 1979), and the mean depth for the specimens sampled is 31.1% SL.

Apart from these modifications, no other data derived from the enhanced *O. machadoi* collection necessitates changes in the generic characters enumerated in Greenwood (1979). The additional material does, however, reinforce earlier conclusions that this species is the least derived member of the taxon (Greenwood, 1979: 298).

As far as I am aware, the new material also provides the first indication, in nature, that any species of *Orthochromis* is a female mouth-brooder (see Staeck, 1983: 178 for comments on the behaviour, in an aquarium, of an unidentified species resembling *O. polyacanthus*). A female *O. machadoi*, 40.5 mm SL, from Folgares (14° 55' S, 15° 06' E) is carrying fry in the buccal cavity. The characteristically distorted buccal cavity in some females from other localities also suggests that these fishes were carrying young at the time of their capture.

*Orthochromis machadoi* (Poll), 1967

SYNONYMY. *Haplochromis machadoi* Poll, 1967. *Publicações cult. Co. Diam Angola* no. 75: 313–315, fig. 152.

*Orthochromis machadoi* (Poll): Greenwood, 1979. *Bull. Br. Mus. nat. Hist. (Zool.)* 35: 295–299.

DESCRIPTION. Based on 35 specimens, 38.0–65.0 mm SL, excluding the type and paratype which were examined previously (Greenwood, 1979). Various characters, such as squamation patterns, fin shape, body form, and dentition were checked on many other specimens, most of which were too distorted to use for morphometric purposes.

Depth of body 27.2–34.5 (M=31.1)% of standard length, length of head 28.5–35.0 (M=32.3%).

Dorsal head profile sloping upwards at an angle of 40°–50° to the horizontal, its outline not broken by the ascending premaxillary processes, and generally straight until a point above the middle of the orbits, after which it is gently curved; in some specimens the lower part of the profile is also slightly curved. The upper margin of the orbit lies distinctly below the level of the dorsal head profile.

Preorbital depth 13.7–29.9 (M=18.2)% of head length; in one extreme individual the preorbital is only 12.5% of head length. Least interorbital width 12.5–20.0 (M=16.0)% of

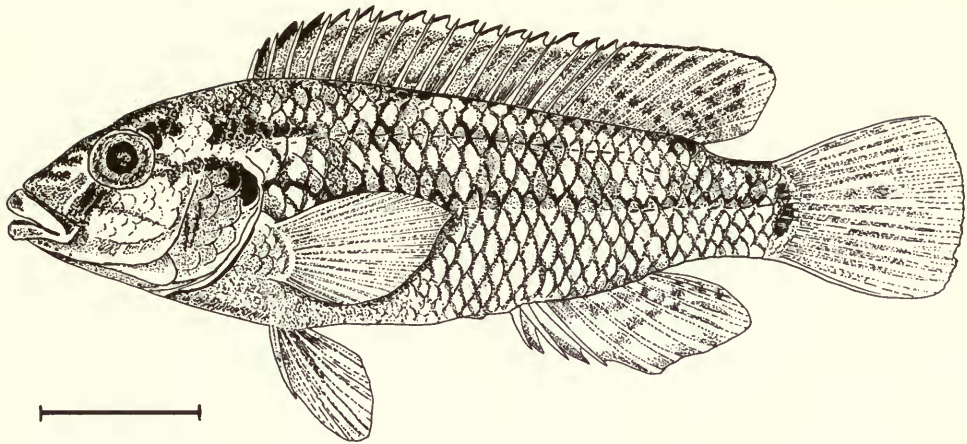


Fig. 9 *Orthochromis machadoi*. Drawn by G. J. Howes. Scale = 20 mm.

head, generally narrower than the preorbital is deep, but occasionally the measurements are equal.

Snout 0.8–1.1 times as long as it is broad (modally 1.0 times), its length 29.2–35.7 ( $M=31.8$ )% of head.

Eye diameter 24.2–33.3 ( $M=28.2$ )% of head, showing no obvious allometry with standard length. Cheek depth 20.8–33.3 ( $M=25.4$ )%.

Caudal peduncle 1.2–1.5 times longer than deep (modally 1.4–1.5 times), its length 15.4–20.5% of standard length.

Mouth horizontal or almost so, the lower jaw generally a little shorter than the upper when the mouth is closed. Lips thickened (but not so noticeably as in *Th. albolabris*) with, in a few specimens, the dorsal margin of upper lip overlapping the ventral margin of the preorbital bone. The posterior tip of the maxilla reaches a vertical through the anterior margin of the orbit or, in a few specimens, extending either a little beyond, or not quite as far as that level. In the latter situation, however, the maxillary tip always reaches to a level well posterior to the nostril.

Lower jaw length 31.0–41.3 ( $M=37.0$ )% of head, and 1.4–1.8 (mode 1.5) times its breadth. The length of the premaxillary ascending processes is 23.8–31.1 ( $M=26.8$ )% of the head.

*Gill-rakers and pharynx.* There are 7 (f2), 8 (f17), 9 (f13) or 10 (f3) gill-rakers in the outer row of the lower part of the first gill-arch; the lower 1–3 rakers are reduced, the others short and stout, and not expanded transversely across the arch; the crown of each raker is simple or, less commonly, crenulate.

The prepharyngeal pads in *O. machadoi* are moderately developed and are comparable with those in the Cunene *Thoracochromis* species, but the pharyngeal epithelium is not noticeably thickened, neither is it distinctly papillate or thrown into longitudinal furrows. Well-developed microbranchiospines are present.

*Scales.* Above the upper lateral-line the scales are weakly ctenoid or cycloid, those below that level are ctenoid except for the cycloid scales on the chest and belly. The chest scales are very small and sharply demarcated in size from those on the ventrolateral aspects of the anterior flanks and belly. The ventromedial scales on the belly are markedly smaller than those on the ventral aspects of the flanks, and show an almost imperceptible size gradient with the scales on the chest (see Greenwood, 1979, fig. 3 for an illustration of the *Orthochromis* chest-belly squamation pattern; the belly scales in *O. machadoi* are relatively larger

than those in the species depicted). Most specimens examined have, bilaterally, a naked area in the chest squamation. The size of this area shows some intraspecific variability, but in no specimen is the entire lateral region of the chest naked.

There are 29 (f1), 30 (f15), 31 (f12), 32 (f4) or 33 (f1) scales in the lateral-line series,  $6\frac{1}{2}$ – $8\frac{1}{2}$  between the upper lateral-line and the dorsal fin origin, 8–11 between the pectoral and pelvic fin bases, and 2–4 (modal range 2–3) rows on the cheek. Cheek squamation pattern is often irregular, but a horizontal naked strip is always present between the scale rows and the preoperculum, as is a small, anteroventrally situated, naked embayment of the scaled area.

There are never more than one large and one small scale between the dorsal fin base and each of the last 6–12 (modally 9–11) pored scales of the upper lateral-line; in one exceptional specimen, however, only the last 3 and 5 scales on the two sides respectively are separated from the fin in this manner, the other scales in the series being separated by 2 large scales of equal size.

*Fins.* Dorsal with 15 (f3), 16 (f20) or 17 (f10) spinous, and 9 (f8), 10 (f20) or 11 (f5) branched rays; anal with 3 (in one specimen 4) spinous and 7 (f1), 8 (f27) or 9 (f5) branched elements. In only 2 of the many specimens examined were traces of anal sheath scales observed (see p. 188), and then only as a single scale in each fish.

Caudal fin rounded or strongly subtruncate, scaled on its proximal half or, rarely, two-thirds.

Pelvic fins with the second branched ray longer than the first, and occasionally, the third also as long as the second; the pelvic spine and the first two rays of the fin are covered by greatly thickened skin.

Pectoral fin 18.3–23.9 (M=21.5)% of standard length, 57.0–81.3 (M=67.2)% of head length.

*Teeth.* In both jaws the *outer row* is composed of relatively slender, close-set and unequally bicuspid teeth (Fig. 2C). Generally from 1–3 slender unicuspid teeth are situated posteriorly in the upper jaw. The number of teeth in the premaxillary outer row varies from 32–50 (modal range 46–50), the number showing weak positive correlation with the fish's standard length.

The *inner series* in both jaws are densely arranged in 2–4 (usually 3 or 4) rows anteriorly and anterolaterally, reducing to a single row posteriorly. The teeth are all tricuspid, with the median cusp slightly larger than the lateral ones.

*Lower pharyngeal bone and dentition.* The dentigerous surface is broader than long (*ca* 1.3 times), and the anterior shaft of the bone is short (Fig. 7C). Its teeth are cuspidate, fine and compressed, with only those in the posterior transverse row noticeably larger and coarser than the others. The teeth in the two median rows are barely coarser than those situated laterally.

*Osteology.* I have been able to compare, intragenerically, the skeleton of *Orthochromis machadoi* only with that of *O. malagaraziensis* (from the Malagarazi river, Tanzania). In all features which could be checked, the two species are virtually identical.

The *neurocranium* (Fig. 10C) is notable for its low supraoccipital crest, fairly steeply sloping (*ca* 45°) dorsal profile, gently rounded transverse profile of the skull roof anterior to the supraoccipital crest, and the slightly convex rather than concave camber to that part of the roof situated between the parietal crests and the base of the supraoccipital crest.

The apophysis for the upper pharyngeal bones is of the *Haplochromis*-type, with small but definite contributions from the basioccipitals.

Expressed as percentages of neurocranial length in the two 13 mm long skulls examined, the orbital depth is 38.0%, the preorbital depth 23.0%, the ethmovermerine length 30.8%, the depth of the otic region 46.0 and 48.5%, the width of the otic region 53.8%, and the height of the supraoccipital crest 15.4% (measured in only one skull).

*Suspensorium* (Fig. 3E). The palatopterygoid region is relatively foreshortened, and the hyomandibula has an expanded anterior flange which extends well beyond the level of the bone's anterior articulatory facet. This expansion of the hyomandibula is probably correlated with the enlarged *levator arcus palatini* muscle. The entopterygoid and palatine bones are in contact.

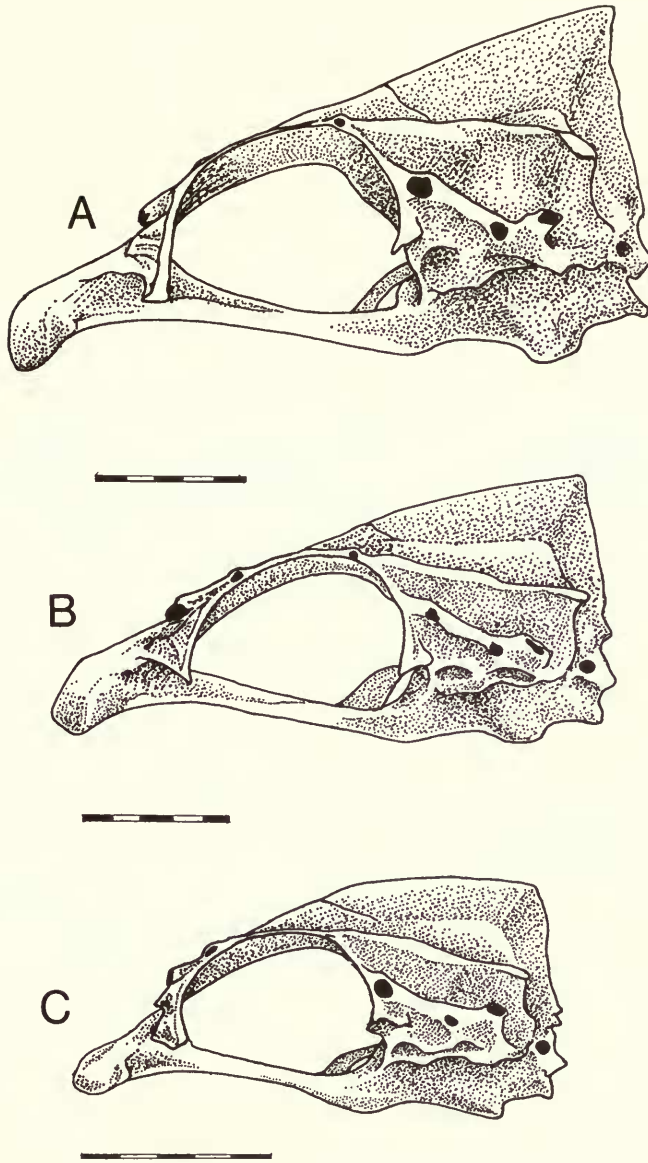


Fig. 10 Neurocranium, in left lateral view, of: A, *Thoracochromis buysi*; B, *Th. albolabris*; C, *Orthochromis machadoi*. Scale in mm.

*Jaws.* The dentigerous arms of the *premaxilla* are slightly inflated, the ascending processes are shorter than the dentigerous arms, and have but a slight posterior inclination (Fig. 8C).

The *lower jaw* (Fig. 11C), as compared with the generalized haplochromine condition, appears foreshortened in lateral view, with the coronoid arm of the dentary originating relatively far forward, and the region surrounding the dentary's division into horizontal and coronoid arms somewhat inflated. The outer tooth row extends posteriorly onto the anterior half, or slightly less, of the coronoid process.

The dorsal gill-arch skeleton was examined in 3 cleared specimens, double stained with alizarin-red and alcian-blue. Its most outstanding feature is the very greatly reduced cartilaginous extension from the anterior border of epibranchial II. In all African cichlids examined so far there is an expansive cartilaginous flange developed from this epibranchial, the flange extending forward and ventrally beyond the head of epibranchial I (see Stiassny, 1981: 294–296, and 1982: 430–432 for an account and figures of this feature in cichlids and related taxa).

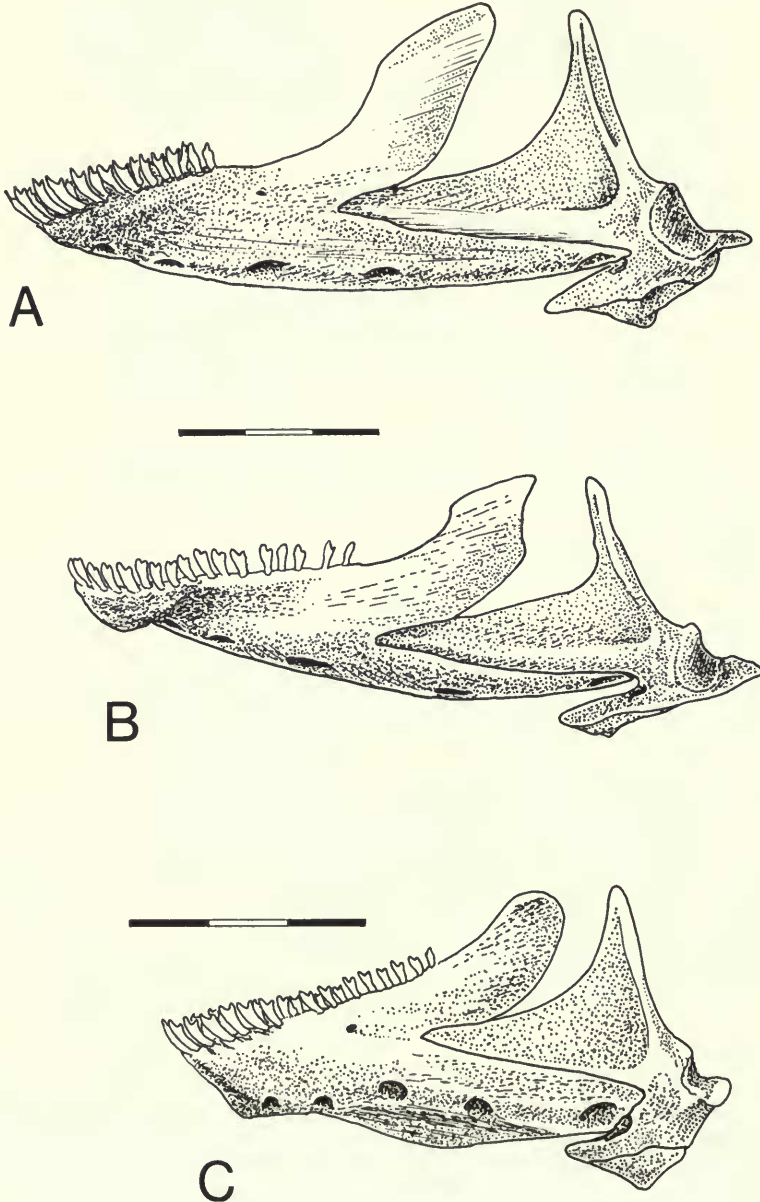


Fig. 11 Lower jaw, in left lateral view, of: A, *Thoracochromis buysi*; B, *Th. albolabris*; C, *Orthochromis machadoi*. Scale in mm.



In *O. machadoi* virtually no such extension is present, the margin of epibranchial II having merely a narrow strip of hyaline tissue (which is partly stained by the alcian blue). The strip is very slightly wider on the right than on the left side of the branchial skeleton, but on neither side is it broader or more extensive than the cartilaginous strip shown by Stiassny (1982: fig. 3) as occurring in the South American species *Cichla ocellaris*.

Regrettably, no double stained preparations are available for other *Orthochromis* species, and the feature cannot be checked on the dry skeletons available. Its significance, phylogenetically speaking, remains to be investigated.

*Caudal fin skeleton.* All eight specimens radiographed have hypurals 1 and 2, and 3 and 4 fused, as do the three alizarin transparencies examined. Such extensive and consistent fusion of hypural elements would seem to be a characteristic feature of the genus *Orthochromis* (Greenwood, 1979: 297).

*Vertebrae.* Excluding the fused  $PU_1$  and  $U_1$  centra, there are 28 (f2), 29 (f17) or 30 (f13) vertebrae, comprising 12 (f21) or 13 (f11) abdominal and 16 (f6), 17 (f20) or 18 (f6) caudal elements.

*Breeding.* As noted earlier, *O. machadoi* is apparently a female mouth-brooder. The smallest sexually active female recorded (apart from the brooding individual) is 46 mm SL, the smallest male, 52 mm. However, the preservation state for the majority of specimens examined precluded accurate determinations of sexual maturity or activity. Hence these figures can give only rough indications of the size at which sexual activity begins.

*Coloration.* Information is only available for formol fixed and alcohol preserved specimens. There are apparently no sexually correlated differences in preserved coloration; sexually active adults of both sexes are represented in the samples studied.

The ground coloration is a light brown (beige), usually shading to yellowish-brown ventrally. There are about twelve broad and dark 'bars' crossing the upper two-thirds to three-quarters of the body's lateral surface, the breadth of the 'bars' being about twice the width of the paler spaces between them. The 'bars' are not solid, but are formed from the dark outlines to the scales underlying the area which they occupy. The centres of these scales are lighter, so that the overall effect is to produce a diamond-mesh pattern of dark reticulations which, in places, are condensed to give the appearance of vertical bars. The centre of each 'bar' is darkest and is somewhat expanded anteroposteriorly, thus creating the appearance of an interrupted mid-lateral stripe; a similar but narrower and fainter stripe runs along the course of the upper lateral-line. At the base of the caudal fin there is a somewhat vertically elongate blotch.

The snout is crossed by two bands, the upper of which is the broader and becomes almost continuous with the darkly bordered scales on the nape and the posterior interorbital regions of the dorsum. A broad and intense lachrymal stripe runs from the orbit to the angle of the jaws, and is continued dorsally as a short blotch above the posterodorsal margin of the orbit. Post-orbitally there is a narrow horizontal bar continuous with the dark dorso-posterior margin of the operculum.

Dorsal, caudal and anal fins are a dusky hyaline, with the dark pigment most concentrated, almost into streaks, between the spinous rays of the dorsal fin. The lappets of that fin are clear. The anal is, apparently, without discrete maculae, and there are no indications of any ocellus-like spots. In males the pelvic fins are dark over their anterior third, and in females are hyaline with a faint dusting of small melanophores over the greater part of their surface.

Within the material examined there is considerable variation in the intensity of dark pigmentation, especially that contributing to the vertical 'bars'. However, within any one sample the intensity is generally constant. Whether this variation is attributable to differing preservation techniques, or is a reflection of populational differences or different environments, remains an open question.

**DISTRIBUTION.** The species is known only from the Cunene river; see also Poll (1967: 23 & 314), and p. 212 for detailed distribution records within the Cunene.

Study material and distribution records of *O. machadoi*

## Registered material

BMNH;	P=collection no.	Locality
1972.9.27:90-91		Cunene R., Ondurusu falls (17° 24' S, 13° 56' E).
1984.2.6:102-103	P612	Cunene R., Ondurusu falls (17° 24' S, 13° 56' E).
1984.2.6:104-108	P1192	Cunene R., Calueque (17° 16' S, 14° 30' E)
1984.2.6:109	P672	Cunene R., 45 miles west of Ondurusu falls (17° 03' S, 13° 30' E).
1984.2.6:110-112	P696	Cunene R., above Epupa falls (17° 00' S, 13° 15' E).
1984.2.6:113	P713	Cunene R., above Epupa falls (17° 00' S, 13° 15' E).
1984.2.6:114-115	P716	Cunene R., above Epupa falls (17° 00' S, 13° 15' E).
1984.2.6:116-131	P1341	Cunene R., 82 km west of Ondurusu falls (16° 59' S, 13° 22' E).
1984.2.6:132-141	P1176	Cunene R., in the Chitapua falls (14° 23' S, 15° 18' E).
1984.2.6:142-145	P918	Cunene R., Folgares (14° 55' S, 15° 06' E).
1984.2.6:146	P882	Cunene R., Folgares (14° 55' S, 15° 06' E).

## Unregistered material

Locality	Number of specimens	Collection no.
Cunene R., 10 miles west of Ruacana falls (17° 26' S, 14° 05' E).	2	P604
Cunene R., 5 km west of Ondurusu falls (17° 24' S, 13° 56' E).	10	P1392
Cunene R., Ondurusu falls (17° 24' S, 13° 56' E).	12	P1481
Cunene R., Calueque (17° 16' S, 14° 30' E).	2	P1192
Cunene R., 32 km west of Ondurusu falls (17° 15' S, 13° 23' E).	7	P1276
Cunene R., 32 km west of Ondurusu falls (17° 15' S, 13° 23' E).	9	P1278
Cunene R., 32 km west of Ondurusu falls (17° 15' S, 13° 23' E).	9	P1296
Cunene R., 32 km west of Ondurusu falls (17° 15' S, 13° 23' E).	17	P1299
Cunene R., Otjinungura (17° 12' S, 12° 20' E).	12	P1843
Cunene R., Otjinungura (17° 12' S, 12° 20' E).	1	P1324
Cunene R., 45 miles west of Ondurusu falls (17° 03' S, 13° 30' E).	12	P670
Cunene R., above Epupa falls (17° 00' S, 13° 15' E).	14	P705
Cunene R., above Epupa falls (17° 00' S, 13° 15' E).	8	P715
Cunene R., above Epupa falls (17° 00' S, 13° 15' E).	2	P697
Cunene R., above Epupa falls (17° 00' S, 13° 15' E).	1	P710
Cunene R., above Epupa falls (17° 00' S, 13° 15' E).	2	P1181
Cunene R., above Epupa falls, and 1 mile east.	4	P708
Cunene R., above Epupa falls, and 1 mile east.	1	P706
Cunene R., 82 km west of Ondurusu falls (16° 59' S, 13° 22' E).	2	P1290
Cunene R., 82 km west of Ondurusu falls (16° 59' S, 13° 22' E).	18	P1341
Cunene R., 82 km west of Ondurusu falls (16° 59' S, 13° 22' E).	10	P1361
Cunene R., 82 km west of Ondurusu falls (16° 59' S, 13° 22' E).	2	P1290
Cunene R., Folgares (14° 55' S, 15° 06' E).	10	P918
Cunene R., Folgares (14° 55' S, 15° 06' E).	13	P1345
Cunene R., Folgares (14° 55' S, 15° 06' E).	4	P882
Cunene R., Chitapua (14° 13' S, 15° 18' E).	2	P1116

DIAGNOSIS AND AFFINITIES. *Orthochromis machadoi* is easily distinguished from other Cunene haplochromines by several features. Amongst these may be noted its very small chest scales which are continuous with the small scales ventrally on the belly; the bilateral naked patches on the chest; the pelvic fins with the second and often the third branched ray longer than the first; the thickened skin covering the pelvic spine and first two or three branched rays; by the absence of discrete spots or ocelli on the anal fin of male fishes, and osteologically, by the low supraoccipital crest, the generally convex dorsum of the skull, and the greatly reduced cartilaginous projection from the anterior face of the second epibranchial bone.

In his original description of the species, Poll (1967: 314) commented on the similarity between the preserved colour pattern of *O. machadoi* and that of *Pseudocrenilabrus philander* (for which see p. 215). The new material of both species from the Cunene river, and elsewhere as well for *Ps. philander*, certainly confirms that similarity (but not the supposed phylogenetic affinity of the two species, as was suggested by Poll). However, the species are readily distinguished by their squamation patterns, especially that on the chest and belly, the sharp size differentiation between chest and ventrolateral flank scales in *O. machadoi*, the nature of the pelvic fins in that species, and in the different modal lateral-line scale counts for the two species (see p. 215 below). Furthermore, *Pseudocrenilabrus philander* is distinguished from *O. machadoi* and all other Cunene haplochromines in having 4 and not 5 lateral-line canal openings in the lachrymal (1st infraorbital) bone.

Despite the large amount of *O. machadoi* material now available, little more can be told about its possible intrageneric relationships (see Greenwood, 1979: 298). The species appears to be the least derived member of the genus, but even that supposition cannot be tested until more is known about its congeners.

### *PSEUDOCRENILABRUS* Fowler, 1934

The diagnosis of this genus is based essentially on ethological features associated with the spawning habits of its constituent species. For details of these see Wickler (1963), in which paper he also erected the genus *Hemihaplochromis*, now treated as a synonym of *Pseudocrenilabrus* (see Trewavas, 1973: 33–36 for a full account of the taxon's nomenclatural history).

The sole morphological reflection of these ethological peculiarities is found in the absence of discrete spots, or of ocelli, on the anal fin of adult males. Instead, these markings are replaced functionally and morphologically by an orange or scarlet tip to that fin, a feature not readily discernible in preserved specimens. There are, however, two other features which, in the context of the Cunene haplochromines, serve to identify the genus, *viz.*, the presence of only four openings in the first bone of the preorbital series (i.e. the lachrymal), and a tendency for there to be some, often several, pore-less scales in the lateral-line series. In those rare specimens with the entire lateral-line pored, only the four-pored lachrymal serves for instant diagnosis. The close superficial resemblance of the preserved coloration in Cunene *Orthochromis* and *Pseudocrenilabrus* species was commented on above; see also p. 215 below.

Currently, three species of *Pseudocrenilabrus* are recognised, *Ps. multicolor* (Schoeller, 1903), *Ps. ventralis* (Nichols, 1928) and *Ps. philander* (Weber, 1897). Their combined distributions extend, latitudinally, from the Nile to Natal, South Africa; no species occurs in north-west Africa.

The species-level taxonomy of *Pseudocrenilabrus* has not been revised for many years, and nothing is known about the phylogenetic relationships of the genus. Three subspecies of *Ps. philander* have been recognised (see Trewavas, 1936: 73, & 1973: 33–36), of which two, *Ps. philander dispersus* (Trewavas) 1936 and *Ps. p. luebberti* (Hilgendorf, 1902) occur within the Angolan region. The former subspecies is found in several rivers, including the

Cunene (Poll, 1967), but the latter is apparently restricted to sink-holes in the neighbourhood of Otavifontein, Namibia.

On the basis of one subspecifically diagnostic feature, the length of the premaxillary ascending process, the Cunene fishes I have examined would be referable to the subspecies *dispersus*, as was the Angolan material examined by Poll (1967). However, the Cunene material has a modal dorsal fin ray spine count of 15, and includes some specimens with 16 spines. On that character it should be referred to the subspecies *luebberti*.

Since these features appear to be the only trenchant ones on which the subspecies can be recognised (Trewavas, 1936: 7, and personal observations), I would argue that there is little to be gained from their formal recognition. A complete taxonomic overhaul of the genus is required, a revision that must take into account coloration and ethological features as well as anatomical ones, and must be based on numerous specimens from many localities. Until that revision is completed, I would also defer any decision on the validity of the third subspecies, *Ps. philander philander* (Weber) 1897, a taxon apparently restricted to Natal and Mozambique.

For these various reasons, and for others noted by Trewavas (1973: 33), the Angolan populations described here are recognised simply as *Ps. philander*.

### *Pseudocrenilabrus philander* (Weber), 1897

SYNONYMY. See Trewavas (1936: 73)

DESCRIPTION. Based on 23 specimens from three localities (see p. 216). Since only ten fishes are undistorted the morphometric analysis is derived from those specimens alone, but meristic data were taken from the whole sample. Also, because of the small sample size, only ranges are given for morphometric characters. Where there are indications of populational differences in certain features, or where these fishes differ from those described by Poll (1967), comments are given between square brackets. Poll's material did include some specimens from the Cunene, but most came from the Cuango, Cuilo and Cassai river systems.

Depth of body 32.9–39.0% of standard length, length of head 34.2–38.8%.

Dorsal head profile sloping at an angle of 40°–45° to the horizontal, straight or gently curved from the nape to a point above the anterior orbital margin, then more strongly curved below that point.

Preorbital depth 12.9–18.2% of head length, the least interorbital width 19.2–25.8%. [Fishes from Jamba bridge, Cutato river, Cubango drainage, have a wider interorbital, 23.1–25.8, mean 21.6% of head, than those from the Cunene river at Calueque and from near Cafu; the range given by Poll for his entire sample is 18.1–24.6%.]

Snout 0.8–1.0 times as long as broad, its length 23.1–33.3% of head length.

Eye diameter 30.8–36.4% of head, cheek depth 16.7–25.0%.

Caudal peduncle 1.1–1.4 times longer than deep, its length 14.5–16.7% of standard length.

Mouth horizontal or almost so, the jaws equal anteriorly when the mouth is closed, the lips slightly thickened. The posterior tip of the maxilla reaches a vertical through the anterior orbital margin, or very nearly so.

Lower jaw 33.1–39.9% of head, 1.2–1.6 times longer than broad. The ascending processes of the premaxilla are 23.1–31.6% of head length.

*Gill-rakers and pharynx.* There are usually 8, rarely 9, short, stout and relatively compressed gill-rakers in the outer series on the lower part of the first gill-arch [Poll's count is 8–10, mode 8]. Microbranchiospines are present and obvious. The pharyngeal epithelium is not greatly thickened, nor is it deeply folded and papillose; the prepharyngeal pads are moderately developed.

*Scales.* There is a very gradual size transition between the scales on the chest and those on the ventrolateral aspects of the flanks and the ventral surfaces of the belly. The chest scales, although smaller than the belly scales, are not markedly smaller.

The lateral line-series has 27–30 (mode 28) scales. [In specimens from the Cutato river, 6–11 scales in the upper lateral-line, and 9–11 in the lower line, are without pores. Specimens from the two Cunene localities (see p. 216) have all the upper lateral-line scales pored, but from 2–7 scales in the lower line may lack openings. Poll makes no comments on this feature.] There are 4–5½ scales between the upper lateral-line and the dorsal fin origin, and 5 or, more frequently 6, between the pectoral and pelvic fin bases. The cheek has 3 rows of large scales which either cover the entire area or have a small naked embayment anteroventrally [Poll gives the range of cheek scale rows as 3–5].

There is never more than one large and one small scale between each of the last 8–14 upper lateral-line scales and the base of the dorsal fin [Poll makes no comments on this feature].

*Fins.* Dorsal with 14, 15 or 16 (mode 15) spinous and 8, 9 or 10 (modally 9 or 10) branched rays, anal with 3 spinous and 7–9 (mode 8) branched elements [The range given by Poll is: dorsal 13–15 spinous and 9–11 branched rays, modes 14 and 10 respectively; anal 3 spinous and 7–9, mode 8, branched rays.] No anal sheath scales were observed.

Caudal fin rounded, scaled on its basal quarter to third. Pectoral fin 22.5–25.4% of standard length, 61.5–69.2% of head length. Pelvics with the first branched ray slightly, but obviously longer than the second ray.

*Teeth.* In the outer row of both jaws the teeth are relatively stout and unequally bicuspid. The minor cusp lies at a slight angle to the broad-based major cusp; posteriorly in the upper jaw the last few teeth usually are unicuspid. There are 28–36 teeth in the outer row of the premaxilla [Poll gives a range of 35 to 63 teeth in this row, and indicates that the number is positively correlated with the fish's length; his sample included specimens longer than any recorded above].

Inner row teeth are tricuspid, with the middle cusp noticeably larger than the others, and are arranged in a single row in each jaw (except for one specimen which has a double row anteriorly and laterally in the lower jaw).

*Lower pharyngeal bone and dentition.* The shaft of the bone is relatively longer than that in any of the Cunene river or other *Thoracochromis* species; its length is contained about 1½ times in the length of the median tooth row (*cf* 1¾–2 times in *Thoracochromis* species). This feature contributes to the less attenuated appearance of the bone when it is compared with that of a *Thoracochromis* specimen.

The dentigerous surface is triangular and equilateral; the teeth are slender, compressed and cuspidate, those of the two median series being only a little coarser than the teeth in the lateral rows [Poll describes the teeth in his material as being 'conique', but I suspect this is an error].

*Osteology.* No skeletal material has been prepared. Vertebral counts (made from radiographs of the Cunene specimens) are: 25 (f1), 26 (f2), 27 (f3) and 28 (f2), comprising 12 (f5) or 13 (f3) abdominal and 13 (f1), 14 (f3) or 15 (f4) caudal elements.

It has proved impossible to produce radiographs suitable for observing the extent, if any, of hypural fusion and apposition.

*Coloration.* Only preserved colours are known for this material. Superficially, the coloration and colour pattern in *Ps. philander* closely resemble those of *Orthochromis machadoi* (see p. 211). They differ, however, in a number of details. The vertical bars on the flanks and caudal peduncle are solid; that is, the entire exposed surface of the scales underlying a bar is pigmented and not, as in *O. machadoi*, only the scale margins. Consequently, the diamond-mesh pattern so characteristic of *O. machadoi* is absent in *Ps. philander*. The bars in *Ps. philander* are less intense than those in *O. machadoi*, except in the region where each is expanded antero-posteriorly to form a faint and horizontal mid-lateral stripe; this restricted area of intensity results in *Ps. philander* having a more intense and discrete mid-lateral stripe. Similarly the upper longitudinal stripe is more distinct in *Ps. philander* than in *O. machadoi*, at least over the anterior half of the stripe's course. The species also differ in having the spot at the caudal fin base in *Ps. philander* less elongate and more distinct than that in *O. machadoi*.

The *dorsal fin* coloration in *Ps. philander* differs in having light spots on a dark background, the spots covering the membrane between the spines, and also in having light, slightly curved and narrow bands sloping obliquely across the dark membrane of the branched dorsal fin; the bands extend, with regular spacing, to the fin's posterior tip. The *caudal fin* also is banded, light on dark, but with the bands arranged vertically. The *anal*, *pelvic* and *pectoral* fins are hyaline, but the anal may be faintly banded by darker stripes running obliquely ventro-dorsad across most of its area. This anal banding is probably confined to males, or at least is more obvious in that sex; it seems to be the only sexually dimorphic feature apparent in the preserved coloration, apart from the faint, light spot at the posterior ventral tip of the anal which is sometimes visible in males.

Like *Orthochromis machadoi*, *Pseudocrenilabrus philander* has a prominent, but narrow, dark lachrymal, stripe; it lacks, however, the well-defined supraorbital continuation seen in *O. machadoi*. Unlike *O. machadoi* there are no transverse bands on the snout, which is dark grey in *Ps. philander*.

**DISTRIBUTION.** Widely distributed in southern Africa; for Angolan localities, see Poll (1967), and below.

**DIAGNOSIS AND AFFINITIES.** See discussion on pp. 213–214 above.

### Study material and distribution records

Museum register number	Locality
BMNH; P=collection no.	
1984.2.6:64–74	Cunene R., pump station at Calueque (17° 16' S, 14° 30' E).
1984.2.6:75–76	Cunene R., near Cafu, Angola (16° 30' S, 15° 10' E).
1984.2.6:77–84	Cutato R., Jamba bridge, Angola (Cubango drainage)
1984.2.6:85–86	Okovango R., at Callindo, Angola

### *SERRANOCHROMIS* Regan, 1920

The *Serranochromis* generic concept was redefined and expanded by Greenwood (1979: 299 *et seq*) to incorporate a number of species previously included in *Haplochromis*. These latter species, some of which had, at an earlier date (Regan, 1920) been placed in the genus *Sargochromis*, are now considered to form a subgenus of *Serranochromis*.

Reasons for uniting these various taxa phylogenetically are given by Greenwood (*op. cit.*), but an additional synapomorphy has been found as a result of comparative studies related to the Cunene representatives of both subgenera. This synapomorphy is the presence, in all species and most individuals, of two to four enlarged median teeth in the first row of the inner premaxillary series; these enlarged teeth are displaced a little anteriorly relative to the others in the row, and so come to lie between the first inner series and the outer tooth row (see figs 4, 9 & 13 in Trewavas, 1964). The majority of specimens I have examined show this displacement quite distinctly, although in a few it may appear only as an obvious irregularity in an otherwise uniformly curved tooth row.

### *SERRANOCHROMIS (SARGOCHROMIS)* Regan, 1920

For a description and diagnosis of the subgenus, and a list of its constituent species, see Greenwood (1979: 303–305).

Considerable difficulty was experienced when attempting to identify the nine

*Serranochromis* (*Sargochromis*) specimens represented in the Penrith collection. Seven of these specimens were collected in the Cunene river, and two are from an affluent of the Cubango river. The latter apparently represent an undescribed species.

The most recent species-level revision of the taxa involved is that by Bell-Cross (1975), who recognised seven species. Only two of these, *S. (Sarg.) giardi* (Pellegrin) and *S. (Sarg.) coulteri* (Bell-Cross) are recorded from the Cunene system, with the latter taxon endemic to it.

Judging from Bell-Cross' descriptions, all seven *Serranochromis* (*Sargochromis*) species are identifiable, when alive, by their distinctive adult male coloration. For preserved material Bell-Cross provides a key employing what, apart from colour differences, seem to be the principal diagnostic features of the taxa. Using this key all the species, either individually or as small groups, should be determinable when, in various combinations, the form of the neurocranial pharyngeal apophysis, the morphology of the lower pharyngeal bone, the nature of its dentition and the shape of the head, are taken into account. Members of species groups, however, are usually separable only on the basis of their geographical distribution. For all species, the ranges of most meristic and morphometric characters show considerable overlap, although there is sometimes a distinction to be found in the mean or modal values for certain features. Such fine distinctions cannot, of course, be utilized when, as in the case of the present collection, only a few specimens are available for study.

From Bell-Cross' key there would seem to be little difficulty in distinguishing between the two species he recognised as occurring in the Cunene, namely *S. (Sarg.) giardi* and *S. (Sarg.) coulteri*. The former is characterized by its massive lower pharyngeal bone with an extensively molarized dentition, and its characteristically 'butterfly'-shaped pharyngeal apophysis (Bell-Cross, 1975: fig. 1 & pp 450–454; also p. 456). In sharp contrast, *S. (Sarg.) coulteri* has a weakly developed lower pharyngeal bone, the teeth of which are '... sharp and pointed' (Bell-Cross, 1975: 455; elsewhere [p. 429] the teeth in the median rows are described as '... slightly enlarged and not molariform'). The pharyngeal apophysis in this species does not depart from the modal *Haplochromis*-type (see Bell-Cross, 1975: fig. 1; also Greenwood, 1978: 303).

I would certainly confirm Bell-Cross' description of the *S. (Sarg.) giardi* pharyngeal bone and dentition, but must disagree with his account of those features in *S. (Sarg.) coulteri*. Using the material (both whole specimens and skeletal preparations) on which Bell-Cross (1975: 426–431) based his description of *S. (Sarg.) coulteri* I find that, apart from the smallest fish in the size range it covers (105–214 mm SL), at least the two median tooth rows, and often most teeth in the next two lateral rows, are composed of enlarged teeth with flat, molar-like crowns and cylindrical necks (Figs 12–15). Morphologically, these teeth are quite distinct from the compressed, shouldered and thus virtually bicuspid teeth occurring in the lateral and posterior dentigerous fields of the bone. Only in the smallest specimen (105 mm SL, BMNH 1975.6.19: 1–13; DA68) do the median teeth retain slight indications of a minor cusp, and a discrete posterior cusp (Fig. 13). In other words, apart from their manifestly coarser appearance, the median teeth in this specimen are like those situated posteriorly and medio-laterally on the bone. This specimen alone, would accord with the description Bell-Cross gives for the pharyngeal dentition in *S. (Sarg.) coulteri*.

Thus, I cannot agree with Bell-Cross' description, in his key, of the pharyngeal teeth in *S. (Sarg.) coulteri* as being 'sharp and pointed' (even the lateral teeth are bicuspid), and would consider his description in the text ('teeth slightly enlarged') to be an understatement, at least with respect to fishes more than 105 mm SL. Likewise, I would argue against his statement (*loc. cit.*) that the crowns are 'not molariform'; they are molariform in large specimens, and could be described as 'submolariform' in all others except the smallest fish.

With that correction made, the situation regarding the specific identification of preserved *Serranochromis* (*Sargochromis*) material is rendered more difficult. The lower pharyngeal dentition in *S. (Sarg.) coulteri* is, in fact, like that in many specimens of supposed *S. (Sarg.) codringtoni* and *S. (Sarg.) mellandi*, and there are no trenchant meristic or morphometric features which can be used to separate elements of the trio.

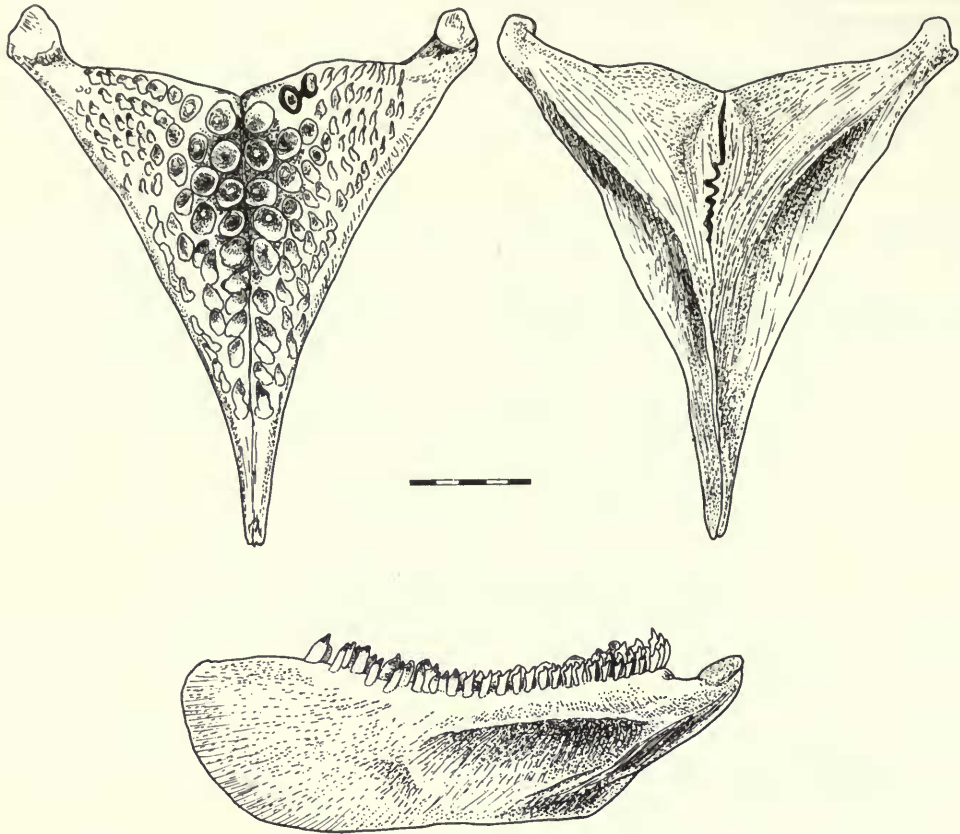


Fig. 12 *Serranochromis (Sargochromis) couleri*. Lower pharyngeal bone of the holotype, a specimen 216 mm SL from the Cunene river system. Scale in mm.

An examination of several specimens identified either as *codringtoni* or *mellandi* shows that there is a wide range in the degree to which the lower pharyngeal dentition is molarized, and a correlated variation in the degree to which the bone is enlarged. In some specimens both bone thickening and tooth molarization exceed that found in *S. (Sarg.) couleri*, but in many others there is complete overlap with the conditions found in that species.

In one respect, overall tooth shape, the enlarged teeth in *S. (Sarg.) couleri* do seem to differ from those in the other two species. Whereas the teeth in *S. (Sarg.) mellandi* and *S. (Sarg.) codringtoni* are short and broad, those in *S. (Sarg.) couleri* are relatively taller and more slender, features particularly obvious in smaller specimens. Also, in *S. (Sarg.) couleri* the posterior horns of the pharyngeal bone appear to be rather more slender than those in the other two species, even when the dentition and bone itself are at comparable levels of hypertrophy.

On the basis of overall pharyngeal tooth morphology, I would therefore refer, at least tentatively, four Cunene river specimens (76.5, 98.0, 130.0 and 132.0 mm SL respectively to *S. (Sarg.) couleri*; for detailed distribution records see p. 230.

These presumed *S. (Sarg.) couleri* differ in some respects from the specimens described by Bell-Cross (1975), but it should be recalled that two are smaller than any of the specimens he examined. In two of the new specimens (76.5 and 98.0 mm SL) eye diameter is larger (30.3% of head length), and the snout is shorter (32.1 and 33.0% head in the specimens



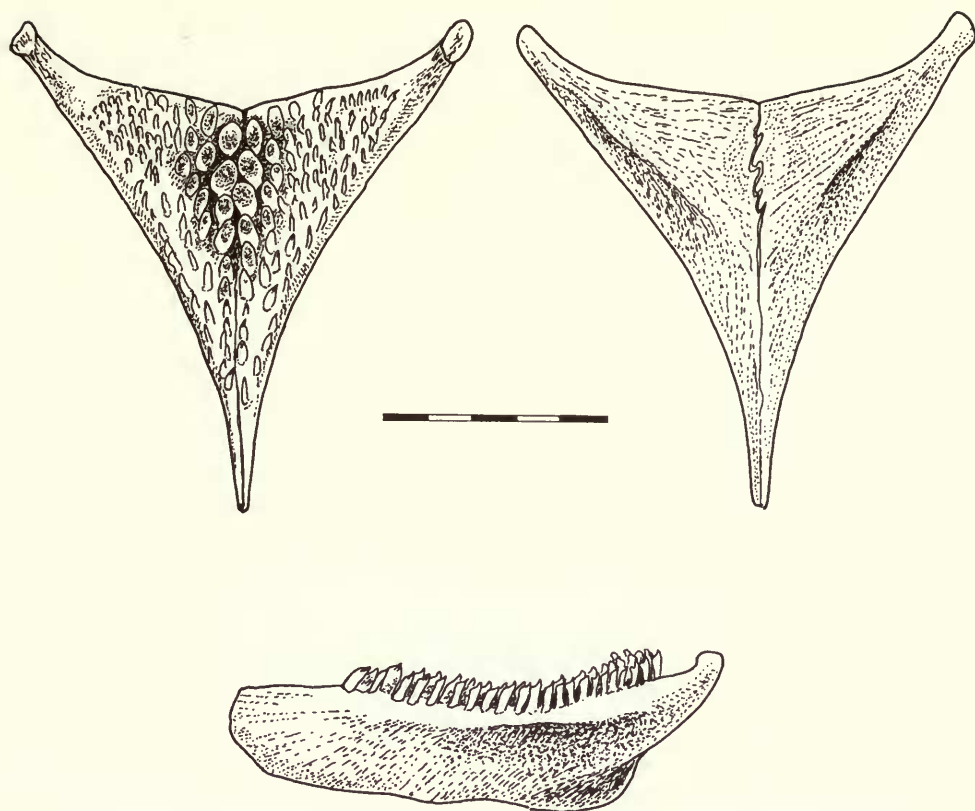


Fig. 13 *Serranochromis (Sargochromis) coulteri*. Lower pharyngeal bone from a specimen 105 mm SL (1975.6.19: 1-3; DA68, ex Cunene river system). Scale in mm.

respectively); the four specimens have slightly shorter lower jaws (33.9–37.0% head of 37.4–42.6% in the Bell-Cross material). All other morphometric features lie within the ranges given by Bell-Cross.

In some meristic characters the new material also lies outside the ranges given by Bell-Cross (1975: table in appendix (iii)). Three of the four specimens (including the two smallest) have 12 or 13 gill-rakers on the first arch (9–11, mode 10, according to Bell-Cross), and all have higher lateral-line scale counts (33 or 34, cf 30–31, mode 31).

Clearly some of these discrepancies might be attributable to personal differences in the way counts and measurements were made, and others could be attributed to the smaller size of two specimens I examined. Parenthetically it should be mentioned that Bell-Cross' (1975: 429) statement that the first branched pelvic ray in *S. (Sarg.) coulteri* reaches the origin of the anal fin, does not hold for specimens other than the type; probably the length of this ray is correlated with an individual's sex and, in the case of adult males, with the level of sexual activity. Also, it should be noted that the photograph of the type specimen reproduced in Bell-Cross (1975: plate 4) was taken before the fish was set and preserved. The distended mouth shown in the picture distorts the dorsal head profile which, in the preserved specimen, is like that in most other *Serranochromis (Sargochromis)* species; see, for example plates 5, 6 and 8 in Bell-Cross (1975).

Of the remaining new *Serranochromis (Sargochromis)* specimens, one large fish (270 mm

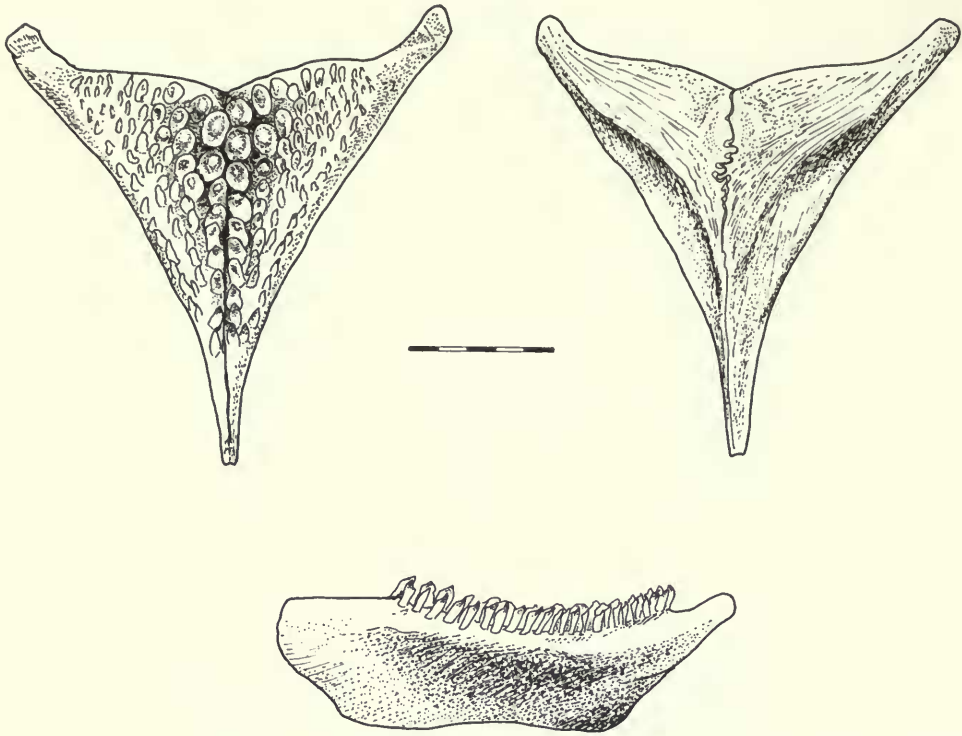


Fig. 14 *Serranochromis (Sargochromis) coulteri*. Lower pharyngeal bone from a specimen 139 mm SL (1975.6.19: 1-3; DA59, ex Cunene river system). Scale in mm.

SL, BMNH 1984.2.8: 1) should, on the basis of its extremely hypertrophied lower pharyngeal bone and the extreme molarization of its teeth (Fig. 16), be identified as *S. (Sarg.) giardi* (see Bell-Cross, 1975: 451-454). In its general appearance too, particularly the almost rounded head profile, this specimen resembles *S. (Sarg.) giardi* from localities outside the Cunene system. However, it differs from those fishes in certain morphometric features, as it does from the few Cunene specimens currently identified as *S. (Sarg.) giardi*. These other Cunene specimens comprise three small fishes (the largest 86.0 mm SL) from Ponang Kuma, Mossamedes (probably Donguena, 17° 03' S, 14° 40' E, according to Dr Michael Penrith, *in litt*). They were previously identified by Boulenger (1915: 408) and by Regan (1922: 263) as *Sargochromis angolensis* (Steindachner), but were reidentified as *Haplochromis giardi* by Bell-Cross (1975).

The new 270 mm long specimen comes from below the Ruacana falls (17° 24' S 14° 13' E) is larger than any of the *giardi* material examined by Bell-Cross, all of which, save that from Ponang Kuma, came from the Okovango, Zambezi or Kafue river systems. It also differs from those specimens in having a greater preorbital depth (26.1% of head *cf* 19.4-22.3, mean 21.2%), and a longer lower pharyngeal bone (43.2% of head, *cf* 37.6-41.8%). The pharyngeal apophysis, however, has the specifically characteristic 'butterfly' shape described by Bell-Cross (1975: 453 and 411; fig. 1), and is of the extreme 'butterfly' type (as might be expected from the great hypertrophy of the pharyngeal mill) which otherwise occurs in fishes from the Zambezi (see Bell-Cross, 1975; fig. 1).

If it be assumed that the deeper preorbital bone (lachrymal), and the longer pharyngeal

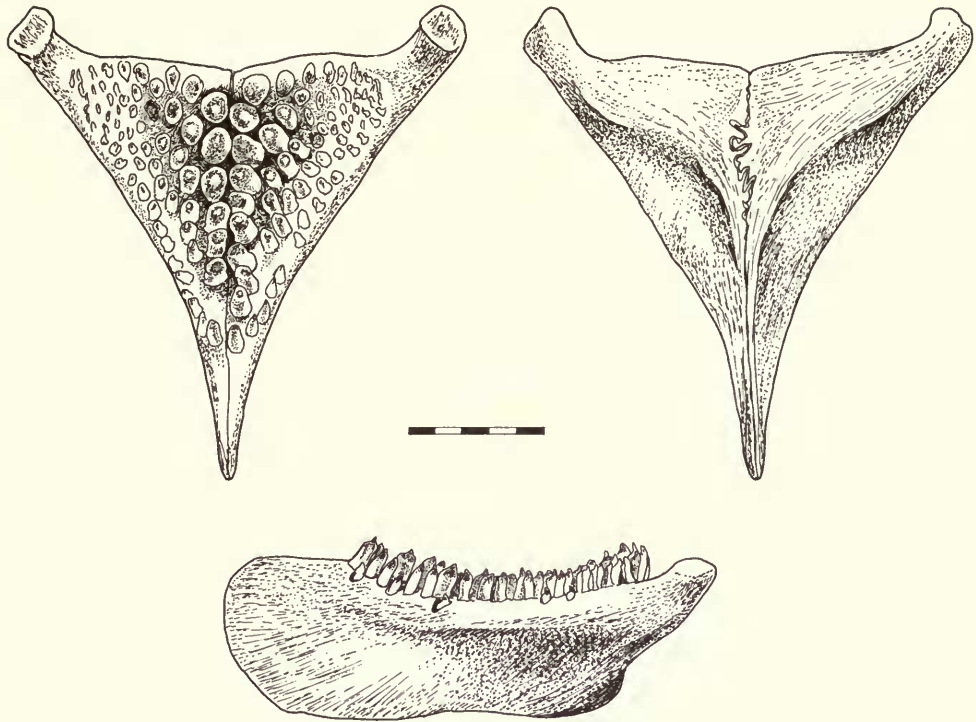


Fig. 15 *Serranochromis (Sargochromis) coulteri*. Lower pharyngeal bone from a specimen 183 mm SL (1975.6.19: 1-13; DA54, ex Cunene river system). Scale in mm.

bone in the new Cunene fish are both correlates of that specimen's large size (or are simply examples of individual variability), this fish could be identified as *S. (Sarg.) giardi*. However, certain other Cunene specimens throw some doubt on that conclusion.

One of these specimens is another large fish, 190 mm SL (BMNH 1984.2.6: 149), and comes from a locality 45 miles west of Ondurusu Falls (17° 03' S, 13° 30' E). It too has an hypertrophied lower pharyngeal bone with an extensively molarized dentition, and its pharyngeal apophysis approaches the extreme 'butterfly' type, being intermediate between the Kafue and Upper Zambezi forms illustrated by Bell-Cross (1975, fig. 1). The lower pharyngeal bone, however, proves to be less massive, and its dentition less molarized than in *S. (Sarg.) giardi* of a comparable size. It is more massive and further molarized than in a 260 mm specimen of *S. (Sarg.) codringtoni*, but only slightly more massive and molarized than in a 194 mm specimen of the same species. Similar results are obtained when the Cunene specimen is compared with examples of *S. (Sarg.) mellandi*.

The 190 mm Cunene specimen, like the 270 mm fish discussed earlier, differs from individuals in other populations of *S. (Sarg.) giardi* in having a deeper preorbital (27.1% of head, cf 18.0-22.0, mean 19.9% in *S. (Sarg.) giardi*) but unlike the larger Cunene fish it also differs in having a somewhat shorter lower jaw (34.2% of head, cf 36.0-42.6, mean 39.6%).

Although the lower pharyngeal bone and dentition in the 190 mm Cunene specimen are comparable, except for the bone's greater length (which does lie within the *giardi* range), with those in some specimens of *codringtoni* and *mellandi*, the short lower jaw would seem to exclude the specimen from either of these taxa, as well as from *giardi*. Its preorbital depth,

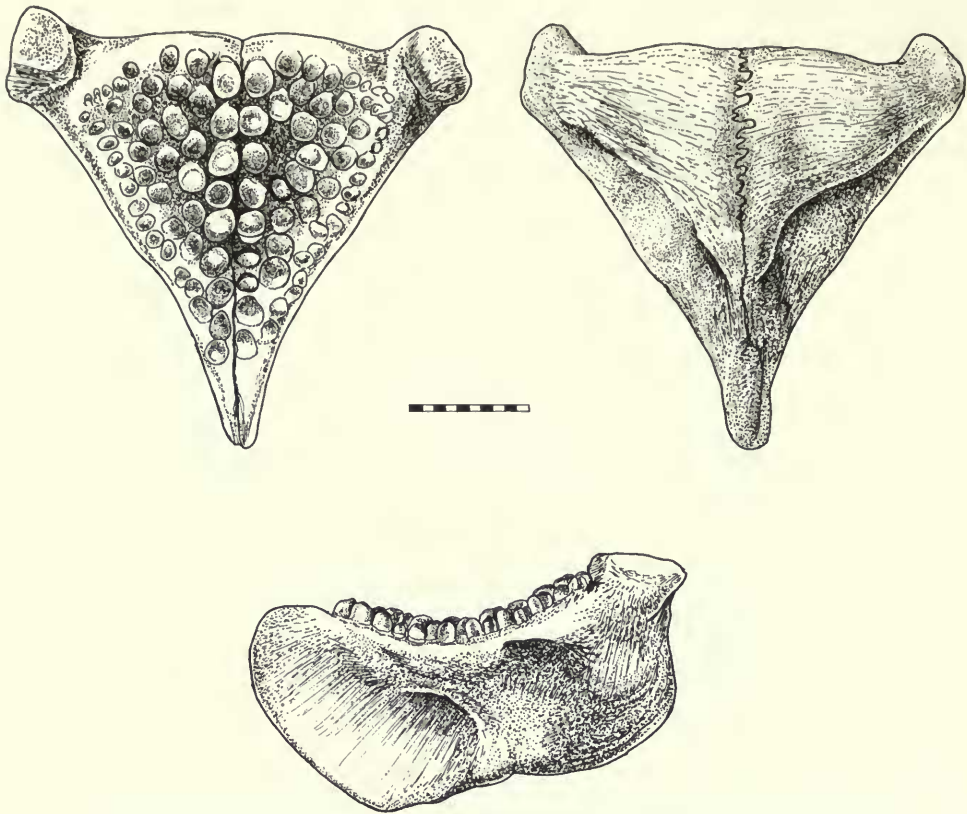


Fig. 16 Lower pharyngeal bone from a *giardi*-like member of the *Serranochromis* (*Sargochromis*) *giardi-codringtoni* species complex, 270 mm SL, ex Cunene river (1984.2.8: 1). Scale in mm.

excessive for *giardi* is, however, only a little greater than the maximum recorded for either *mellandi* or *codringtoni*.

The larger (270 mm) specimen, it will be recalled, has a more massive pharyngeal mill than is found in specimens of either *mellandi* or *codringtoni*, but that 'gap' is bridged by the bone and its dentition in the 190 mm fish. Lower jaw length in the larger fish, however, lies within the ranges for *giardi*, *codringtoni* and *mellandi*, and its preorbital depth lies within the ranges for *codringtoni* and *mellandi*, but outside that for *giardi*. In other words, on morphometric characters and in the nature of the pharyngeal mill, the two *giardi*-like fishes from the Cunene seem to show, either in the themselves or by providing bridging features, characters of three *Serranochromis* (*Sargochromis*) species, only one of which (*giardi*) is thought to occur in that river.

This situation is by no means clarified when two further specimens, 122 and 190 mm SL, from the Hamburg Museum collections, are taken into account. These fishes (ZMH 1722, collected in the Cunene at Capelongo) have greatly hypertrophied lower pharyngeal bones with extremely molarized dentitions. On those criteria the specimens fall within the range of variation encountered within *S. (Sarg.) giardi*, *mellandi* and *codringtoni* (Fig. 17) but are perhaps nearest *giardi*. The length of the bone (33.5% of head length) for the larger of the two Hamburg specimens, however, is below that for *giardi* of a comparable length, is near but slightly shorter than that for *codringtoni*, and is well within the range for *mellandi*. The

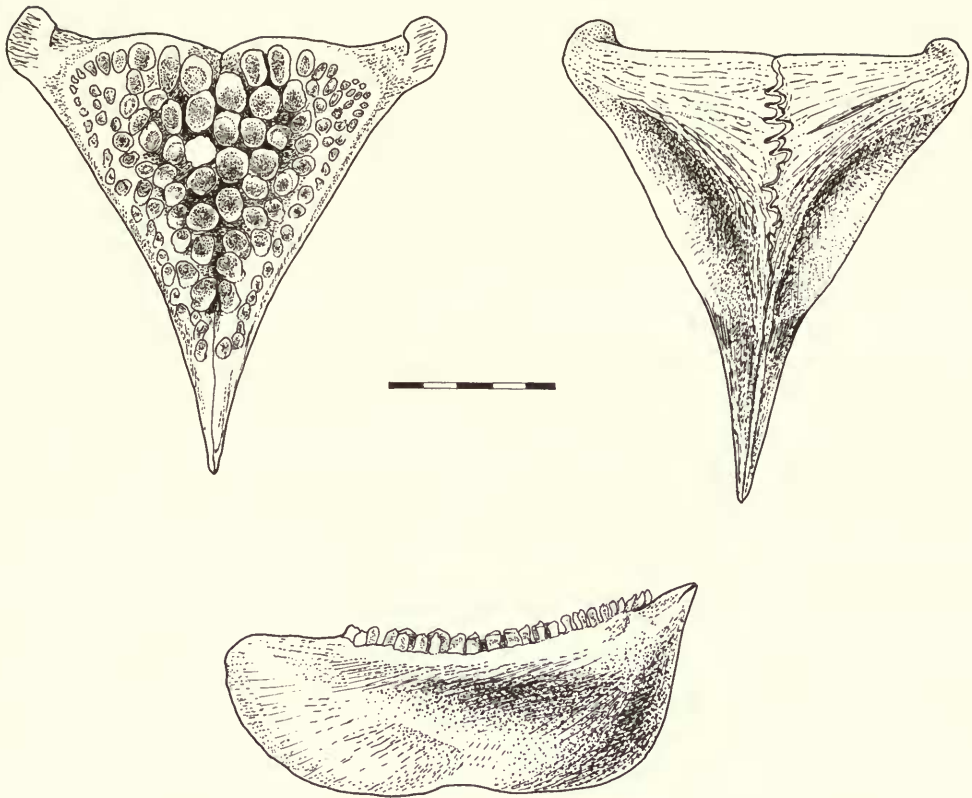


Fig. 17 *Serranochromis* (*Sargochromis*) *codringtoni*. Lower pharyngeal bone from a specimen 183 mm SL (1975.6.19: 1-3; ex Kafue river). Scale in mm.

length of the bone in the smaller fish, 33.3% of the head, falls within the recorded ranges for comparable sized *mellandi* and *codringtoni*, but is below that for *giardi* of the same length.

Preorbital depth in the larger Hamburg specimen (25.0% of head) is somewhat greater than that recorded for *giardi*, but closely approaches that for *codringtoni* and *mellandi*; in the smaller fish, the preorbital depth (21.0% of head) lies within the range for comparable sized *giardi*, *codringtoni* and *mellandi*.

Lower jaw length in the larger Hamburg fish (35.8% of head) is slightly below that of *giardi*, and also below that of *codringtoni*, but is much shorter than in *mellandi*; the smaller specimen, however, has a jaw length (38.0% of head) within the ranges for all three species.

Taken in concert, the features in the two Hamburg specimens, and those of the two Cunene fishes, certainly seem to break down the principal morpho-anatomical differences between *Serranochromis* (*Sargochromis*) *giardi* and *S. (Sarg.) codringtoni*, and, indeed, those between these species and *S. (Sarg.) mellandi*.

This conclusion casts doubts on any possibility of identifying the new Cunene specimens with enlarged pharyngeal mills. The small specimens from Ponang Kuma (see above, p. 220) can be identified as *giardi* on the basis of various 'key' characters. But, in the absence of specimens at sizes intermediate between them and the larger fishes discussed above, even that identification is uncertain.

Clearly the situation is confused, and is unlikely to be clarified without studying a lot more material, supported by data on breeding coloration, from all areas in which the species *giardi*, *mellandi* and *codringtoni* have been recorded. Until that revision is effected, I would prefer to recognize the Cunene specimens with hypertrophied pharyngeal mills only as members of a *Serranochromis* (*Sargochromis*) *giardi-codringtoni* species-complex, that complex to include *S. (Sarg.) mellandi*. Certainly it would be unrealistic to refer the Cunene specimens to any one species in that complex; to describe them as a new species would confuse the issues involved.

I suspect that specimens from Lake Calundo, Angola, described by Poll (1967) and identified by him as *Haplochromis mellandi*, are also members of the '*giardi-codringtoni*' complex. Poll's figure (1967: fig. 50, p. 310), and his remarks about the deep preorbital in these fishes, reinforce my suspicions. Bell-Cross (1975: 436) thought that Poll's specimens should be referred to *S. (Sarg.) codringtoni*, a taxon which I would include in the complex under discussion.

At this point it is appropriate to mention certain type specimens of Boulenger's (1913) species *Tilapia steindachneri* (see p. 189). The specimens in question (BMNH 1907.6.29: 176-9; from the Donguena swamps) were later referred to *Sargochromis mellandi* [now *Serranochromis (Sargochromis) mellandi*] by Regan (1922: 263), a decision with which I would concur, allowances being made for the species-level problems discussed above. All are small fishes (52.0-64.0 mm SL). One, the largest, was illustrated by Boulenger (1915: 210; fig. 134) and designated 'Type' in the caption to the figure accompanying this redescription of the species. That action I treat as the subsequent designation of a type specimen since none was chosen when the species was first described (Boulenger, 1913).

The figured specimen and three others from Donguena swamp are easily distinguished from the remaining syntypes of *Tilapia steindachneri*, collected in the Que river, a tributary of the Cunene. The Que fishes are now referred to *Thoracochromis buysi* (Penrith); see p. 190.

The type and three syntypes of *Tilapia steindachneri* from Donguena swamp have enlarged lower pharyngeal bones, with most teeth in the two median rows enlarged and molariform or submolariform, and thus resemble those in *Serranochromis (Sargochromis) codringtoni* and *S. (Sarg.) mellandi*. Considering the small size of these fishes, and the degree to which their lower pharyngeal bones are enlarged, it seems likely that, as adults, they would have relatively massive to massive pharyngeal bones, and a highly molarized dentition. Unfortunately there is no way in which the four specimens can be given a positive specific identification, especially in the light of what is now known about the possible complex of *Serranochromis (Sargochromis)* species in Angola (see p. 217). Under the circumstances it would seem inadvisable to consider the synonymy of *Tilapia steindachneri* (in part) with *Serranochromis (Sargochromis) mellandi* as well established. The question should be left open until the Angolan '*giardi-codringtoni*' complex is resolved. From that complex could well emerge a taxon which would take the name '*steindachneri*'.

Finally, attention must be given to another *Serranochromis (Sargochromis)* specimen amongst the new material from the Cunene river. This fish, 126 mm SL (BMNH 1984.2.6: 154) is apparently referable to the species *S. (Sarg.) greenwoodi* (Bell-Cross), a taxon not previously recorded from Angola; all other records are from the Upper Zambezi, Kafue and Okavango river systems. Apart from the new species to be described below, *S. (Sarg.) greenwoodi* is unique amongst the species of this subgenus in having, at least in most populations, a fine lower pharyngeal bone with no noticeably enlarged or molarized teeth (see Bell-Cross, 1975: 425).

The Cunene specimen, from Matala Dam, Luceque (14° 36' S, 15° 18' E) is an adult male. It has a relatively slender lower pharyngeal bone (length 27.6% of head length) whose dentition is composed mainly of fine bicuspid teeth; a few teeth in the posterior part of the two median rows are somewhat enlarged, but, like the others, are distinctly bicuspid. In all morphometric features, including a deep preorbital bone (27.6% of head), long snout (42.5% of head), long lower jaw (42.5% of head), and long ascending premaxillary processes (34.5% of head), the specimen falls within the range for *S. (Sarg.) greenwoodi* from other localities.

Its dental and meristic characters are also within the range of that species, and include the high gill-raker count of 14. Despite our apparently identical methods for counting the lateral-line scale series (Bell-Cross, 1975: 410), I make the number of scales in *S. (Sarg.) greenwoodi* 33–36, and not, *pace* Bell-Cross, 29–31. The Cunene fish has a count of 33.

Although this fish resembles *S. (Sarg.) greenwoodi* in all features ascertainable from a single, preserved specimen, its precise status will be uncertain until more material is available, and data are obtained on the live colours of breeding males.

The two remaining *Serranochromis (Sargochromis)* specimens in the Penrith collection were obtained from the Cubango river drainage basin. They are conspecific, but do not seem referable to any of the species or populations so far described.

I am loath to create a new taxon on only two specimens, especially since the taxonomy of the subgenus *Sargochromis* is in such an uncertain state. However, the specimens are very distinctive and thus would seem to justify their recognition as members of a new species.

*Serranochromis (Sargochromis) gracilis* sp. nov.

(Fig. 18)

**HOLOTYPE.** An adult female, 116.5 mm standard length, from the Cutato river at Jamba bridge (Cubango drainage), Angola; BMNH 1984.2.6: 147. **Paratype:** an adult female 118.0 mm SL, from the same locality; BMNH 1984.2.6: 148.

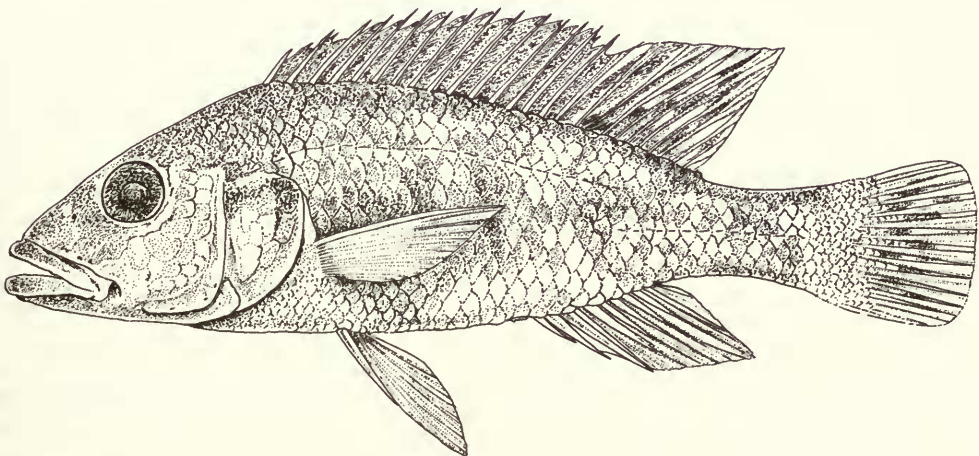
The trivial name, from the Latin, meaning slender or simple, refers to the body proportions of the type specimens, and to the relatively unspecialized nature of the pharyngeal dentition.

**DESCRIPTION.** Based on the two types specimens only.

Depth of body 33.1 and 34.3% of standard length, length of head 36.9 and 37.3%.

Dorsal head profile gently curved and sloping at an angle of *ca* 30°–35° to the horizontal.

Preorbital depth 18.6 and 19.3 of head length, least interorbital width 18.2 and 18.6%. Snout 1.1 and 1.2 times longer than broad, its length 31.8 and 33.7% of head. Eye diameter 25.0 and 25.6% of head, depth of cheek 22.7 and 23.3%.



**Fig. 18** *Serranochromis (Sargochromis) gracilis*. Holotype. Drawn by G. J. Howes. Scale = 18 mm.

Caudal peduncle 1.4 and 1.5 times longer than deep, its length 15.4 and 16.1% of standard length.

Mouth very slightly oblique, sloping at an angle of *ca* 15° to the horizontal; lips slightly thickened, jaws equal anteriorly when the mouth is closed. Posterior tip of the maxilla reaching a vertical through the anterior orbital margin; premaxilla not beaked anteriorly, its ascending processes breaking, slightly, the dorsal outline of the head, their length 31.8 and 32.5% of the head.

*Gill-rakers.* Ten in the outer row on the lower part of the first gill arch, the lowest one or two rakers greatly reduced, the following 5 or 6 either stout and short (holotype) or relatively slender, the uppermost 3 rakers either flattened, with the crown produced into 2 or 3 cusps, or flattened and anvil-shaped (holotype). Microbranchiospines are present.

*Scales* on the anterior part of the body below the lateral-line are weakly ctenoid, but are cycloid above that level. Scales on the posterior part of the body are cycloid. When ctenoid, the scales have the cteni distributed over most of the exposed parts. The chest scales are not noticeably small, and have a gradual size gradient with those on the belly and ventrolateral aspects of the flanks.

Lateral-line with 34 scales, cheek with 4 rows of large scales which cover the area except for a small naked embayment anteroventrally. There are 5 scales between the dorsal fin origin and the lateral-line, 7 between the pelvic and pectoral fin bases. Only the last (holotype), or the last two, pored scales of the upper lateral-line are separated from the dorsal fin base by one large and one small scale, the others being separated from the fin by at least 2 large scales of almost equal size.

*Fins.* Dorsal with 15 spinous and 13 branched rays, anal with 3 spines and 10 branched elements. No anal sheath scales are present in either specimen. Pectoral fin 22.3 and 22.9% of standard length. Caudal subtruncate, scaled over its basal two-thirds or three-quarters. First branched pelvic ray not reaching the vent.

*Teeth.* The *outer row* in both jaws is composed of relatively slender and compressed teeth. In most the crown has a sharp, fine point and a low, laterally placed shoulder; other teeth in the row are more distinctly bicuspid, the shoulder being replaced by a discrete minor cusp. Posteriorly, there is a short edentulous region on the premaxilla. About 50 and 54 teeth are present in the premaxillary outer row.

The *inner teeth* are mostly tricuspid or weakly bicuspid, but a few unicuspid occur anteriorly; the teeth are arranged in a single row in both jaws, that of the upper jaw extending posteriorly beyond the anterolateral section of the bone's dentigerous surface. Medially in the upper jaw there are two enlarged teeth situated between the inner and outer tooth rows.

*Lower pharyngeal bone and dentition* (Fig. 19): The bone is not enlarged, its teeth are distinctly cuspidate, with the minor cusp present as either a well-demarcated shoulder or a discrete cusp. Teeth in the two median rows are manifestly coarser and larger than those situated laterally and postero-laterally. The dentigerous area is a little longer than broad, giving it a more nearly isoscelene than equilateral outline. The length of the bone, measured in one specimen, is 28.0% of the head length.

*Osteology.* No skeleton is available but both specimens were radiographed. Excluding the fused PU<sub>1</sub> and U<sub>1</sub> centra, there are 31 vertebrae, comprising 15 abdominal and 16 caudal elements. In the one specimen dissected the neurocranial pharyngeal apophysis is of the typical *Haplochromis*-type, although the basioccipital contributions to the facet are not extensive.

Judging from the radiographs, the neurocranium has a relatively protracted ethmovomerine region. Comparison with figures in plates 1 & 2 of Bell-Cross (1975) suggests that of the skull of *S. (Sarg.) gracilis* is nearest that of *S. (Sarg.) greenwoodi*, a resemblance confirmed by comparisons with actual skulls.

*Coloration.* Live colours are unknown. The two formol preserved and alcohol fixed specimens have a pale beige ground coloration which darkens dorsally and lightens ventrally; the dorsal surface of the head and snout is greyish. Traces of up to eight vertical bars cross the flank and caudal peduncle, and are most obvious over the midlateral surfaces of the flanks;



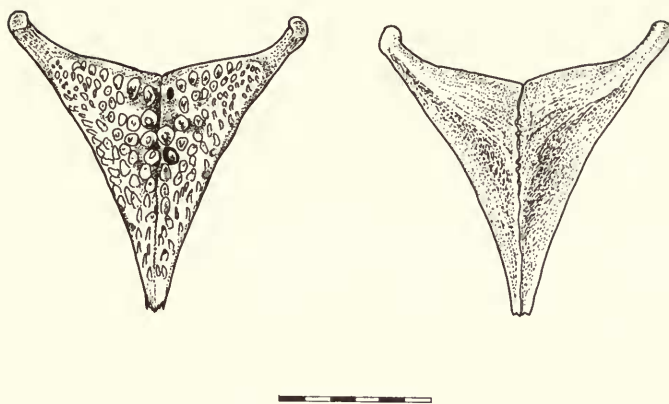


Fig. 19 *Serranochromis (Sargochromis) gracilis*. Lower pharyngeal bone. Scale in mm.

dorsally the bars merge with the darker ground colour, ventrally they terminate along a horizontal line drawn posteriorly from the base of the pectoral fin. A pronounced opercular spot is present, but no other cephalic markings are apparent.

The entire *dorsal fin* is densely flecked with brownish to reddish streaks and elongate spots, the markings becoming more discrete on the soft parts of the fin; the lappets to the spinous dorsal have a similar dark pigmentation. The *caudal fin*, to about its distal quarter, is darkly spotted with elongate ovoid maculae; the distal quarter of the fin is hyaline, with traces of a dark but narrow marginal band, more obvious in one specimen than the other. The *pectoral*, *pelvic* and *anal fins* are hyaline; the soft part of the anal is lightly maculate, the spots fairly regularly arranged in two rows.

*Breeding*. Both specimens are adult females at an advanced stage of oogenesis; the left and right ovaries are equally developed.

**DISTRIBUTION.** Known only from the Cutato river, Angola.

**DIAGNOSIS.** The relatively slender, unthickened lower pharyngeal bone of *S. (Sarg.) gracilis*, with its distinctly bicuspid teeth, sets the species apart from all members of the subgenus except *S. (Sarg.) greenwoodi* and some individuals of *S. (Sarg.) coulteri* (see p. 217).

The compressed outer row teeth in the jaws, the persistence in that row of bi- and weakly bicuspid teeth in specimens over 100 mm SL, and the persistence in such individuals of numerous tricuspid teeth in the inner tooth rows, distinguish *S. (Sarg.) gracilis* from both *S. (Sarg.) greenwoodi* and *S. (Sarg.) coulteri*, and from the other species as well. The gently sloping dorsal head profile, and the shallow body of *S. (Sarg.) gracilis* are further diagnostic features.

More specifically, *S. (Sarg.) gracilis* is distinguished from the two species with fine pharyngeal bones and dentition as follows:

From *S. (Sarg.) greenwoodi* by its shorter pectoral fins (22.3–22.9% SL *cf* 25.6–29.2, mean 27.7%), shorter snout (31.8–33.7% head, *cf* 37.4–40.7, M = 39.3%), shallower preorbital bone (18.6–19.3% head, *cf* 25.3–27.3, M = 26.3%), narrower interorbital width (18.2–18.6% head, *cf* 21.4–13.9, M = 22.8%), and by its fewer gill-rakers (10 *cf* 12–15, mode 15).

From *S. (Sarg.) coulteri* it is distinguished, apart from differences in the pharyngeal bones, by its shorter pectoral fins (22.3–22.9% SL, *cf* 25.4–29.3, M = 27.3%), much shorter snout (31.8–33.7% head, *cf* 36.9–40.4, M = 38.7%), slightly shallower preorbital depth (18.6–19.3% head, *cf* 20.6–22.1, M = 21.4%), and somewhat longer lower jaw (44.2–46.6% head, *cf* 37.4–42.6, M = 39.6%).

**AFFINITIES.** It is difficult to suggest any phylogenetic relationships for *S. (Sarg.) gracilis* within the *Sargochromis* assemblage. In part this is because virtually no anatomical information is available for the new species, and in part because it seems to share no uniquely derived features with any other member of the group. The characters which it does share with *S. (Sarg.) greenwoodi* and *S. (Sarg.) coulteri*, in particular those shared with the former species, appear to be plesiomorphic ones associated with the generalized type of pharyngeal jaws present in both taxa. For the moment *S. (Sarg.) gracilis* can only be considered a possible candidate for sister-species relationship with *S. (Sarg.) greenwoodi*. If that were established, the two species would then constitute a sister group to all other *Serranochromis* species. The relationships of *S. (Sarg.) coulteri*, because of its relatively derived pharyngeal dentition, would be with other members of the subgenus.

### ***SERRANOCHROMIS (SERRANOCHROMIS)* Regan, 1920**

For a description and diagnosis of the subgenus see Greenwood (1979: 299 *et seq.*).

Two species, *Serranochromis (Serranochromis) thumbergi* (Castelnau) and *S. (S.) macrocephalus* (Blgr) are represented in the Penrith collection. Several of the specimens were badly distorted in preservation, but it has been possible to identify them by using a combination of various and mutually exclusive characters. Because of their poor preservation no detailed descriptions of the species can be given. The material differs little from that described by Trewavas (1964) from other localities, but where differences were observed, or could be observed, these will be noted.

In the distribution maps published in her monograph, Trewavas (1964) records *S. (S.) thumbergi* and *S. (S.) robustus jallae* from the Cunene (*op. cit.*: fig. 26), and *S. (S.) macrocephalus*, with *S. (S.) angusticeps*, from a short, isolated and westward flowing river north of the Cunene (*op. cit.* figs 27 & 28 for the species respectively). This river opens to the sea near the town of Mossamedes. Since the Angolan material which Trewavas lists for the two latter species (*op. cit.*: 34 & 40) bears only the locality 'Mossamedes', her indication of their occurrence near that town seems reasonable enough (as would, for the same reason, her record of *S. (S.) robustus jallae* in the same river). However, according to Dr Penrith (*in litt.*)... 'A problem with some early collections, especially Ansoerge's, has been the use of Mossamedes. This could refer to the town of that name; it could and usually did, refer to the district, a district that in the nineteenth century comprised most of southern Angola. Maps show two rivers flowing into the sea near Moçamedes, the Bero and the Giraul, and a third, the Curoca, entering the sea slightly further south. None of these rivers is perennial, and with the exception of some isolated stretches are dry for much of the year. Most older references to "Mossamedes" therefore probably refer to the Kunene river'.

The same doubt must affect the presumed localities for certain Angolan *S. (S.) robustus* specimens. These were also collected by Ansoerge from 'Mossamedes', and on Penrith's arguments could have come from the Cunene river, thus casting doubt on Trewavas' record of the species in the small river north of the Cunene. Other *S. (S.) robustus* material collected by Ansoerge, however, is from Donguena, and therefore is definitely attributable to the Cunene river system, as is the Hamburg Museum specimen (ZMH 1718) from Mülongo-Fürt. Possibly we should accept with reservation the presence of *S. (S.) robustus*, *S. (S.) macrocephalus* and *S. (S.) angusticeps* in the small northern river indicated on Trewavas' (1964) maps until their presence is confirmed by further collections.

No specimens identifiable as *S. (S.) angusticeps* are included in the new collection, but the identification of two Cunene river specimens, collected by Ladiges in 1959 (ZMH 1300 & 1307), as *S. (S.) angusticeps* can be confirmed.

#### ***Serranochromis (Serranochromis) thumbergi* (Castel.)**

For the species as a whole, Trewavas (1964: 24 & 26) described the coloration of specimens

preserved in alcohol. She noted that vertical markings on the body may be absent or, if present, are much fainter than the longitudinal ones, and are confined to the upper part of the body. Two of the four Cunene specimens (168–183 mm SL; all from the Matala Dam, Luceque) have the vertical bars predominating, while the two other fishes have the longitudinal midlateral stripe as the dominant component. In one of the latter specimens, both the vertical and horizontal markings are faint, and equally so.

The total vertebral counts (excluding the  $PU_1$  and  $U_1$  centra) in all four specimens is 36, comprising 18 abdominal and 18 caudal elements in three specimens, and 19 and 17 centra respectively in the fourth fish. These figures are in agreement with those given by Trewavas.

The identity of two *S. (S.) thumbergi* specimens in the Hamburg Museum (ZMH 1719) was confirmed. Both were collected by Ladiges from the Cunene river at Capelongo, Angola (14° 55' S, 15° 06' E). In one, the horizontal markings of the colour pattern predominate, but in the other, the horizontal and longitudinal components are equally intense.

### *Serranochromis (Serranochromis) macrocephalus* (Blgr)

Only one large specimen (160 mm SL; from Luceque) is represented in the collection, the remaining 21 individuals are much smaller (31–110 mm SL) and come from a number of different localities (see below, p. 230).

It is regrettable that the majority of small specimens are so badly distorted as to render them unsuitable for morphometric analysis. Little information is available on allometric and other growth changes in any *Serranochromis* species.

Total vertebral counts (excluding  $PU_1$  and  $U_1$ ) in the specimens radiographed, which included the largest and the smallest fish, are 32 (f11) and 33 (10), comprising 15 (f11) or 16 (f10) abdominal and 16 (f4), 17 (f13) or 18 (f4) caudal elements. Trewavas (1964: 29) gives the total counts in this species as 31–33, and the range for abdominal centra as 15 or 16; the only caudal count she records is 17 (all these figures are adjusted from Trewavas' original counts so as to exclude  $PU_1$  and  $U_1$  centra). The low number of abdominal vertebrae in *S. (S.) macrocephalus*, and hence the low total count, serves as a further feature distinguishing this species from the superficially similar *S. (S.) robustus jallae*.

One of the specimens examined (from a locality 45 miles west of Ondurusu Falls) is unique amongst all the *Serranochromis (Serranochromis)* specimens in the collection in having anal sheath scales present (see p. 188 above).

### *Serranochromis (Serranochromis) angusticeps* (Blgr) and *S. (S.) robustus jallae* (Blgr)

As noted earlier, neither of these species is represented in the new collection. However, the presence of both species in the Cunene river has been confirmed on the basis of specimens in the Hamburg Museum collections (see p. 189).

### Zoogeographical considerations

Before considering what light the new material might throw on the zoogeography of the Cunene river fish fauna, attention must be given to four species which Poll (1967: 23) lists as occurring in that river. The species involved are *Haplochromis darlingi* (Blgr), *H. angolensis* (Steindachner), *H. frederici* (Castelnau) and *H. mellandi* (Blgr). The last named species has been discussed already in connection with the Cunene *Serranochromis (Sargochromis)* (p. 224).

The presence of *Haplochromis darlingi* (now *Pharyngoichromis*; see Greenwood, 1979: 310), a species otherwise known only from the Zambezi, is based on Poll's redetermination of specimens first identified by Pellegrin (1936: 60) as *Pelmatochromis welwitschi*. Poll (*op. cit.*) also identified several more specimens from various Angolan rivers as *H. darlingi*. His

### Study material and distribution records for *Serranochromis (Sargochromis)* species

Museum register number		Locality
BMNH; P=collection no.		
<i>giardi-codringtoni</i> complex		
1984.2.8:1		Cunene R., below Ruacana falls (17° 24' S, 14° 13' E).
1984.2.6:149	P 984	Cunene R., 45 miles west of Ondurusu falls (17° 03' , 13° 30' E).
<i>couleri</i> :		
1984.2.6:150	P809	Cunene R., nr Cafu (16° 30' S, 15° 10' E).
1984.2.6:151	P1094	Cunene R., Matala dam at Luceque (14° 36' S, 15° 18' E).
1984.2.6:152	P1095	Cunene R., Matala dam at Luceque (14° 36' S, 15° 18' E).
1984.2.6:153	P1120	Locality unknown.
<i>greenwoodi</i> :		
1984.2.6:154		Cunene R., Matala dam at Luceque (14° 36' S, 15° 18' E).

### Study material and distribution records for *Serranochromis (Serranochromis)* species

Museum register number		Locality
BMNH; P=collection no.		
<i>thumbergi</i> :		
1984.2.8:2	P1551	Cunene R., at Luceque (14° 40' S, 15° 07' E).
1984.2.8:3.	P1091	Cunene R., Matala dam at Luceque (14° 36' S, 15° 18' E).
1984.2.8:4	P1093	Cunene R., Matala dam at Luceque (14° 36' S, 15° 18' E).
1984.2.8:5	P1096	Cunene R., Matala dam at Luceque (14° 36' S, 15° 18' E).
<i>macrocephalus</i> :		
1984.2.8:6-12	P665	Cunene R., 45 miles west of Ondurusu falls (17° 03' , 13° 30' E).
1984.2.8:13-17	P669	Cunene R., 45 miles west of Ondurusu falls (17° 03' , 13° 30' E).
1984.2.8:18	P670	Cunene R., 45 miles west of Ondurusu falls (17° 03' , 13° 30' E).
1984.2.8:27	P899	Cunene R., Calueque (17° 16' S, 14° 30' E).
1984.2.8:19-20	P808	Cunene R., Calueque (17° 16' S, 14° 30' E).
1984.2.8:21	P1092	Cunene R., Matala dam at Luceque (14° 36' S, 15° 18' E).
1984.2.8:22-23	P1116	Cunene R., Chiatapu (14° 23' S, 15° 18' E).
1984.2.8:24-26	P1179	Cunene R., Jamba-ia-Homa (13° 46' S, 15° 30' E).

description of these fishes, in particular the presence of large anal spots in males, led me to express some doubts about their true identity (Greenwood, 1979: 311). Now, having examined some of Poll's material (from Lake Calundo; MCA: 163987-986), these doubts are reinforced. Certainly the specimens do resemble *Ph. darlingi* in some respects, but the anal fin markings are unlike those of Zambezi *Ph. darlingi*, while the lower pharyngeal bone and dentition in the Angolan fishes are, respectively, less well-developed and less molarized. Thus, at least until more is known about intraspecific variation in Zambezi *darlingi*, and until the live coloration of specimens from Angola and elsewhere is recorded, I would defer any inclusion of *Ph. darlingi* amongst the haplochromine species of Angola. The Angolan '*darlingi*', I suspect, probably represents an undescribed species distinct from that in the Zambezi, and one whose phylogenetic and hence generic relationships are at present indeterminable.

Poll's inclusion of *Haplochromis angolensis* in the Cunene fauna stems from Boulenger's (1915: 409) identification of three specimens from Mossamedes as that species. It is these specimens which Bell-Cross (1975: 451) reidentified as *Haplochromis giardi*, and which are discussed on page 220 above. The single type specimen of Steindachner's *angolensis* is now lost (see Bell-Cross, 1975: 426) and the true identity of the taxon is unlikely to be determined because the original description is totally inadequate for that purpose. The inclusion of *angolensis* in the Cunene faunal list would, therefore, seem to be rendered null and void. As a result of Bell-Cross' reidentification of the specimens involved, the record for *H. angolensis* should be replaced by one for *Serranochromis (Sargochromis) giardi*. But, as discussed on p. 224 above, there are certain doubts about the specific identity of *giardi*-like fishes in the Cunene.

The record for *Haplochromis frederici* (now *Serranochromis [Sargochromis] greenwoodi*, see Bell-Cross, 1975, and Greenwood, 1979) was presumably based on Ladiges' (1964: 268) identification of four fishes from Capelongo as *H. frederici*. I have examined these specimens (ZMH 1722), and find that two (190 and 122 mm SL) should be referred to the *Serranochromis (Sargochromis) giardi-codringtoni* complex (see p. 222) and that the other two (132 and 76 mm SL) can be referred, provisionally, to *S. (Sarg.) couleri* (Bell-Cross). Interestingly, *S. (Sarg.) greenwoodi* is present amongst the new Cunene material (see p. 224).

The new cichlid material from the Cunene river, and the taxonomic changes which it has necessitated, throw very little fresh light on the zoogeographical relationships of the river's haplochromine fauna (but see, Appendix II).

The species of *Serranochromis (Serranochromis)* occurring in the Cunene also occur in the Upper Zambezi system (including the Okovango river), the Kafue, the Upper Zaire drainage, and in the other Angolan rivers. At the species, but not the subspecies-level, one taxon *S. (S.) robustus* extends to Lake Malawi and the Shire river (see Trewavas, 1964 and 1973; Poll, 1967).

Because of the confused species-level taxonomy of *Serranochromis (Sargochromis)*, little zoogeographical information can be derived from the species of that subgenus in the Cunene. It seems likely, nevertheless, that their relationships are with taxa from the Zambezi and Kafue systems, the Cunene fishes being either conspecifics or, if specifically distinct, their vicariant counterparts.

The genus *Pseudocrenilabrus* has an extraordinarily wide distribution in Africa (Nile, Lakes Victoria, Edward, George and Malawi, the Zambezi, Limpopo and Zaire basins, various Angolan rivers, the Okavango and Orange rivers, and the rivers of Natal and Kwazulu). Once again, inadequate species-level taxonomy precludes any fine zoogeographical analysis (see p. 214). The Cunene and other populations of *Pseudocrenilabrus* appear to be referable to *Ps. philander*, a species with a wider, but more southerly distribution than its congener *Ps. multicolor* which is confined to the Nile, Lakes Victoria, Edward, George and to streams and small lakes in Uganda. The Cunene *Pseudocrenilabrus* species is certainly quite distinct from *Ps. ventralis*, a species endemic to the Zaire river (Nichols, 1928).

That several of the Cunene and other Angolan haplochromines previously classified in the genus *Haplochromis* are now referred to *Thoracochromis* (p. 189) is possibly of some

biogeographical significance. *Thoracochromis* has a wide distribution encompassing the Nile (including Lake Albert), Lake Turkana, Lakes Edward and George, Lake Mweru, and the lower Zaire drainage system (see Greenwood, 1979: 293). It has not so far been found in the Zambezi. The two Cunene species, *Th. buysi* and *Th. albolabris*, are both endemic to that system; unfortunately their phyletic relationships cannot yet be determined.

Morphologically, *Th. buysi* is a generalized species, and could well be the local, that is vicariant member of a group including at least two other Angolan taxa, *Th. lucullae* and *Th. schwetzi*. There are indications from the material I have examined that other species will eventually be added to the group.

*Thoracochromis albolabris*, in sharp contrast, is a highly derived taxon (see p. 204) whose specialized features, being autapomorphic ones, do not help in establishing its relationships within the genus. Certainly there are no characters indicative of affinity with any Zairean taxa, nor with its Angolan congeners. Indeed, the only relationship suggested is with *Melanochromis labrosus* of Lake Malawi (see p. 205). That possibility cannot be elaborated further until more is known about the anatomy and osteology of *M. labrosus*.

Finally, there is *Orthochromis machadoi*, another endemic species, and a member of another genus with Zairean connections (see Greenwood, 1979: 297). Unlike *Thoracochromis*, *Orthochromis* is otherwise confined to the Upper Zaire system (extending that drainage, in an historical context, to include the Malagarazi river which now empties into Lake Tanganyika).

*Orthochromis machadoi* is the least derived member of the genus, and thus cannot be linked, as a sister-species, with any of its congeners. Its colour pattern suggests a possible affinity with *O. malagaraziensis* of the Malagarazi river, Tanzania (see Greenwood, 1979: 298), but the value of that character for establishing a true phyletic relationship is still untested.

In brief, and on a broad scale, it seems that the new collection corroborates earlier suggestions of the Cunene cichlid fauna's affinities with those of the Zambezi and Zaire systems (Trewavas, 1964 & 1973; Bell-Cross, 1975; Roberts, 1975). Any finer resolution of those affinities will depend on the acquisition of many more data leading to greater precision in establishing interspecific relationships. For the moment it is much easier to recognise differences, that is endemism, than it is to assess phylogenetic affinities.

Any remarks made about levels of endemism for particular rivers in Angola must perforce be cautious ones since the area is still poorly collected. The situation is also complicated by the absence of precise locality data for some apparently 'good' species currently represented by one or a few specimens. From the information now available, the Cunene has at least four endemic haplochromine species, namely, *Orthochromis machadoi*, *Serranochromis (Sargochromis) coulteri*, *Thoracochromis buysi* and *Th. albolabris*, and there are indications of two or possibly three other endemic species as well. Even without the inclusion of these undescribed taxa, the Cunene has the highest number of endemic haplochromines for any Angolan river (see Poll, 1967; Trewavas, 1973).

Several difficulties are encountered when attempting to compare the Cunene haplochromine fauna with that of other rivers in Angola, in particular those which flow westward and empty directly into the Atlantic. In part these problems stem from the inadequacy of existing collections, and in part from the poor documentation of earlier collections. For example, as species occurring in westward flowing rivers, other than the Cunene, Poll (1967: 23) lists, under the generic name *Haplochromis*, the taxa *acuticeps*, *fasciatus*, *humilis*, *lucullae*, *multiocellatus* and *welwitschi*. The type locality for *acuticeps* is recorded only as Angola, and the species has not since been identified in material from any westward flowing river. Likewise, *humilis*, known from the holotype only, has not been recorded since its original description; again, the type locality was given merely as Angola. *Haplochromis fasciatus* (now *Thoracochromis*) does not appear to have been collected in any westward flowing Angolan river (pace Poll's reference to Regan [1922], who cites its distribution only as 'Lower Congo'). There are doubts about the identity of certain specimens referred to the species by Regan (see Greenwood, 1979: 293), but the types are from the lower Zaire drainage.

Poll's (*op. cit.*) listing of *Haplochromis welwitschi* in western rivers other than the Cunene is probably attributable to uncertainty about the exact provenance of the holotype, for long the only known example of the species. It seems likely that, apart from Poll's specimens taken in tributaries of the Cubango river (Zaire drainage) and other Angolan rivers flowing into the Zaire system, the only other recorded locality for the species is the Cunene river (see Appendix II).

Finally, there is the problem of *Haplochromis angolensis*. This is discussed fully on p. 220. In brief, the specimens to which Poll refers were misidentified by Boulenger (1915), and anyhow came from the Cunene drainage and not one of the other westward flowing rivers in which Poll records the species' presence.

Thus, in effect, Poll's list of five haplochromine species in western rivers other than the Cunene is reduced to two, *lucullae* and *multiocellatus*; these taxa may be referred to as 'small haplochromines' in contradistinction to those whose individuals reach a much larger adult size (that is, species of *Serranochromis*). The 'small haplochromines' are represented in the Cunene by three endemics, *Thoracochromis buysi*, *Th. albolabris* and *Orthochromis machadoi*, and the non-endemic *Pseudocrenilabrus philander*. Using adult size as a criterion, the non-endemic *Chetia welwitschi* (see Appendix II) should also be included as a Cunene 'small haplochromine'. If what appear to be two undescribed species (so far represented by inadequate samples) are also included, the total number of Cunene 'small haplochromine' species is seven, five more than in any of the other westward flowing rivers of Angola.

For the 'large haplochromines' in the other rivers, Poll (1967: 23) lists a total of five taxa, *viz* four species of *Serranochromis* (which would now be referred to the nominate subgenus of that taxon), and *Haplochromis mellandi* (now referred to the subgenus *Sargochromis* of *Serranochromis*). The four *Serranochromis* (*Serranochromis*) species also occur in the Cunene (see p. 228 above). Because of the confused situation surrounding the taxonomy of Angolan *Serranochromis* (*Sargochromis*) species it is not certain whether *S. (Sarg.) mellandi* occurs in the Cunene, or, indeed, whether it is present in Angola at all. A *mellandi*-like taxon is present in some Angolan rivers, and may be in the Cunene as well. It is possible that five *S. (Sargochromis)* taxa occur in that river, namely a *giardi*-like and a *mellandi*-like species, together with *S. (Sarg.) coulteri*, a species close to, if not conspecific with *S. (Sarg.) greenwoodi* and *S. (Sarg.) gracilis*.

Thus, from the data currently available, the Cunene haplochromine fauna, in terms of species numbers, is probably richer than that of all the other westward flowing rivers combined, and also richer than that of those rivers which ultimately flow into the Upper Zaire river basin.

Indeed, at the species level, haplochromine diversity in the Cunene is higher than in the Zambezi-Kafue system, a situation attributable mainly to the greater number of 'small haplochromine' species present in the Cunene, three of which are members of Zairean genera (*Thoracochromis* and *Orthochromis*) not represented in the Zambezi and Kafue rivers.

In conclusion it can be noted that the genus *Pseudocrenilabrus* is present in the Cunene, but not in other westward flowing rivers of Angola, whilst *Hemichromis* which does occur in those rivers (Poll, 1967) is apparently absent from the Cunene. The reverse pattern to that of *Hemichromis* holds for *Orthochromis*, a genus represented in the Cunene by the endemic *O. machadoi*, but one which seemingly is absent from other Angolan rivers emptying directly into the Atlantic. Possibly these paradoxes could be resolved if more was known about the ecological requirements of the species involved.

## Appendix I

The generic status of various Angolan species referred to *Haplochromis* by Regan (1922), Poll (1967), Trewavas (1973) and Bell-Cross (1975)

Four species in this category have now been placed in the genus *Thoracochromis*, see pp. 189–206 above. The generic status of certain other species was reviewed in Greenwood

(1979). There, reasons were given for transferring *H. thysi* Poll (1967) and all the 'large *Haplochromis*' species revised by Bell-Cross (1975) to the subgenus *Sargochromis* of *Serranochromis*. Also in that paper, *H. machadoi* Poll (1967) was recognised as an *Orthochromis* species (see also p. 206 above).

The generic status of the other Angolan '*Haplochromis*' species remains uncertain.

*Haplochromis humilis* (Steindachner), 1866, recorded only as being from Angola, is not currently available for reexamination (see p. 189). Bell-Cross' (1975: 426) comments, coupled with Steindachner's original description and accompanying figure, suggest that the specimen should probably be referred to a species of *Serranochromis* (*Sargochromis*).

The type of *H. angolensis* (Steindachner), 1865 is lost (see Bell-Cross, 1975: 426); the original description is so inadequate that the type specimen's identity cannot be determined at either generic or specific levels.

The type and only specimen of *Haplochromis multiocellatus* Blgr, 1913 has a gradual size-change of scales in the transition area between chest and belly squamation. Such a pattern would exclude the species from *Thoracochromis* (see Greenwood, 1979: 290), a genus with which it shares no other diagnostic features either. That the type appears to have true anal ocelli of the kind found in *Astatotilapia* and in the majority of Lake Victoria haplochromines (see Greenwood, 1979: 274-5), would also seem to argue against its inclusion in *Thoracochromis*. However, details of anal fin markings are difficult to ascertain in preserved specimens, and the absence of true ocelli in all *Thoracochromis* species has yet to be established on the basis of fresh or live material. Thus, the generic status of '*Haplochromis*' *multiocellatus* must remain undetermined, except in so far as it cannot be referred to the genera *Haplochromis*, *Thoracochromis* or *Serranochromis* as defined by Greenwood (1979). At a lower taxonomic level, it should be recalled that Trewavas (1973: 31) believes the taxon to be a junior synonym of '*H. acuticeps*' (whose generic status is, at least for the moment, also uncertain (see above, p. 190)).

*Haplochromis welwitschi* (Blgr) 1898, is discussed in Appendix II.

## Appendix II

### The generic status of *Pelmatochromis welwitschi* Blgr, 1898

Surprisingly, this species has never been formally transferred to any other haplochromine genus, despite the fact that it clearly is not a member of the genus *Pelmatochromis* as currently defined, and despite its obvious membership of the genus *Haplochromis* as defined by Regan (1920 & 1922). It has, however, been referred to as *Haplochromis welwitschi* by several workers, notably Poll (1967), Trewavas (1964) and Bell-Cross (1975).

When reviewing the generic status of fluviatile haplochromine species (Greenwood, 1979: 310 & 313), I commented on the possible generic affinities of *P. welwitschi*, particularly in the light of Trewavas' (1974: 9; fig. 1) suggestion that it might be related to *Serranochromis* (Greenwood, 1979: 306).

At that time I considered whether the species might be included in the genus *Chetia* Trewavas (1961) but expressed reservations about its formal transfer to that taxon until further material could be studied. Having now had the opportunity to examine specimens from Angola, kindly lent to me by the MRAC, I would withdraw those reservations.

My reasons for doing so are based on *Chetia flaviventris*, type species of the genus, sharing with *P. welwitschi* a number of character combinations which neither genus shares with other haplochromine taxa. These include dental characters, features of the squamation pattern, vertebral numbers, and the type of spotting on the anal fin of male fishes. The recently described *Chetia mola* (see Balon & Stewart, 1983) also shares these features, differing only in its hypertrophied pharyngeal jaws and dentition, and in correlated modifications to the neurocranial apophysis for the upper pharyngeal bones.

The entirely unicuspid oral dentition of available *welwitschi* specimens is like that in larger



*Chetia flaviventris* specimens. In *C. flaviventris*, the unicuspid outer row teeth appear in specimens of a very small size (see Trewavas, 1961); since none of the *welwitschi* material is less than 100 mm SL, it is not possible to check whether this species, too, shows a similar precocity in dental ontogeny. Neither *welwitschi* nor *C. flaviventris* has enlarged and serially displaced median teeth in the inner premaxillary tooth row (see p. 216).

Apart from the last 1 to 4 scales in the upper lateral-line series, all the scales in that row of both species are each separated from the dorsal fin base by at least one small and two large scales of equal size, comparable in that respect with the pored scales below them.

The lower pharyngeal bone in *C. flaviventris* and in *welwitschi* is fine and relatively narrow, with long and delicate (*welwitschi*) or relatively delicate posterior horns (cf Fig. 20 with fig. 19 in Greenwood, 1979). None of the median row teeth in *welwitschi* is much coarser than the teeth situated laterally in the dental field, but in *C. flaviventris* some median teeth are slightly coarser than those elsewhere on the bone. The morphology of the pharyngeal teeth is similar in both species; only those teeth in the posterior half of the dental field have a well-marked shoulder or a distinct minor cusp, the others being essentially unicuspid with a sharp and oblique crown.

Like *C. flaviventris*, *P. welwitschi* has numerous spots on the anal fin of male fishes. In the holotype of *P. welwitschi*, now faded, there are about 8–10 spots arranged in a short upper and a longer lower row; the MRAC specimens examined have an estimated 13–15 spots, in several irregular rows, scattered over the greater part of the fin, but these fishes are larger than the holotype (see p. 237 below).

Finally, both *C. flaviventris* and *welwitschi*, when compared with all the other fluviatile haplochromine species except *Serranochromis*, show a tendency towards an increase in the number of abdominal vertebrae (see Greenwood, 1979). The three *welwitschi* specimens all have 14 or 15 abdominal elements, most of the *C. flaviventris* examined have 15, although 14 were counted in one.

It must be stressed that none of the distinctive characters shared by *Chetia flaviventris* and *P. welwitschi* is uniquely synapomorphic for the two species (see Greenwood, 1979: 308–310

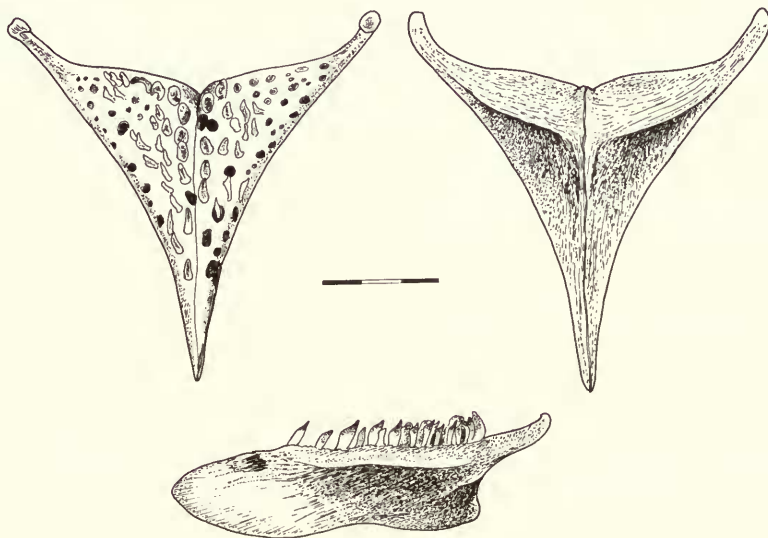


Fig. 20 *Chetia welwitschi*. Lower pharyngeal bone. Numerous teeth are missing, but their sites of attachment are indicated. Scale in mm.

for further discussion). Taken together, however, the various characters appear to be shared only by these two species and *C. mola*. Since none has any detectable feature or features shared uniquely by it and any other genus, it would seem reasonable to consider them congeneric until such times as their implied monophyly can be refuted. There would certainly seem to be no grounds for recognising *welwitschi* as representing a distinct lineage, and thus a distinct genus.

*Chetia welwitschi* (Blgr) 1898

SYNONYMY. *Pelmatochromis welwitschi* Boulenger, 1898. *Proc. zool. Soc. London*: 149, pl. xix; *idem*, 1915. *Cat. Afr. Fw. Fishes*, 3: 397, fig. 268.

*Haplochromis welwitschi*: Trewavas, 1964. *Annls Mus. r. Congo Belg*, Ser. 8vo, Zool. no. 25: 1-58; Poll, 1967. *Publicações cult. Co. Diam. Angola* no. 75: 1-381; Bell-Cross. 1975. *Occ. Pap. natn. Mus. Rhod.* ser. B. 5 (7): 405-464; Greenwood, 1979. *Bull. Br. Mus. nat. Hist. (Zool.)* 35 (4): 265-322.

DESCRIPTION. Poll (1967: 307-309; fig. 149) gives a detailed account of the Angolan material he examined. The table and comments below refer only to the holotype (BMNH 1864.7.13: 62) and the two Angolan specimens from Sanguenque Uembe Cûanaa, Angola, loaned by the MRAC (154779-780), which were not included in Poll's (1967) redescription of the species.

In three morphometric features (smaller eye, deeper preorbital and longer lower jaw), the MRAC specimens differ slightly from the holotype, but these discrepancies could be due to the larger size of the former. There is, however, a marked discordance in caudal peduncle length when Poll's (1967) figures for other material are compared with those obtained from

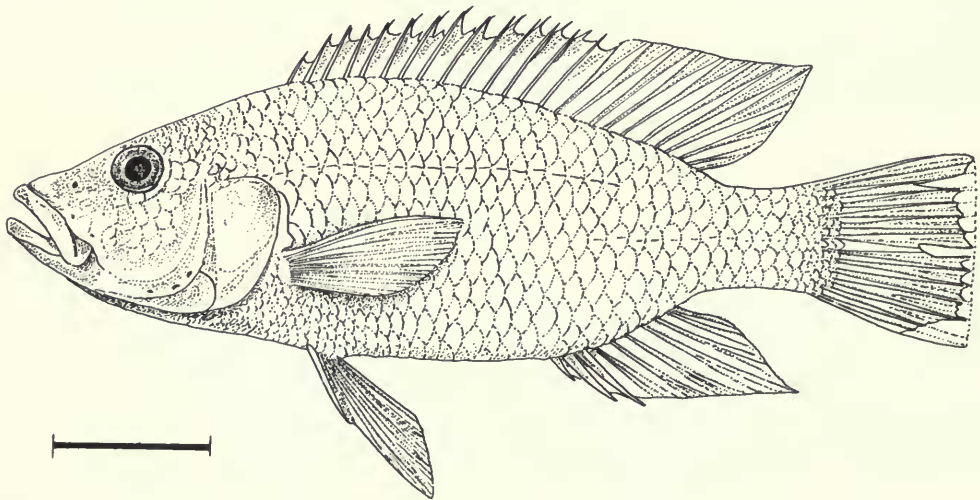


Fig. 21 *Chetia welwitschi* (Blgr). Holotype; after Boulenger (1915). Drawn by G. J. Howes. Scale = 20 mm.

the specimens described above. Poll gives the caudal peduncle length as 30.0 and 32.6% of the standard length; one can only conclude that these figures are typographical errors.

There are 34 scales in the lateral-line series of the holotype, and 32 in the MRAC specimens. In the original description, Boulenger (1898) gives a count of 32 for the type, but this was changed to 33 in his 1915 description of the species. No anal sheath scales are present in the MRAC fishes, but a few scattered scales, on both sides of the fin, are preserved in the holotype. None was found in the type and two paratypes of *Chetia flaviventris* I examined.

	Holotype BMNH:1864.7.13:62	MRAC Specimens 154779-780	
Standard length	102.0	126.0	146.0
Depth of body*	33.3	34.1	34.2
Length of head*	32.3	34.1	34.2
Preorbital bone depth†	24.3	20.9	21.0
Least interorbital width†	21.2	23.3	22.0
Snout length†	36.3	34.9	34.0
Snout length/breadth	1.1	1.0	0.9
Eye diameter†	22.8	18.6	20.0
Cheek depth†	33.3	32.6	32.0
Lower jaw length†	42.5	47.1	48.0
Lower jaw length/breadth	1.7	1.8	2.0
Caudal peduncle length/depth	18.6	17.0	17.5
Caudal peduncle length/breadth	1.4	1.5	1.5
Length of premaxillary ascend. processes†	33.0	30.2	30.0
Pectoral fin length*	18.1	20.6	20.5
†	56.0	60.5	60.0

\* = percentage of standard length; † = percentage of head length

The holotype of *C. welwitschi* has 9 short and relatively stout gill-rakers on the lower part of the first gill-arch; there are 9 rakers in one of the MRAC specimens, and 11 in the other. Microbranchiospines are present in all three fishes, but are smaller and less obvious in the holotype.

Many outer row teeth are missing in the holotype, but I would estimate that about 40 were once present in the premaxilla. There are about 56 premaxillary teeth in the MRAC specimens (Poll [1967] gives a count of 68 in the two fishes he examined).

The holotype has 30 vertebrae (excluding the fused PU<sub>1</sub> and U<sub>1</sub> centra), comprising 15 abdominal and 15 caudal elements; the two other specimens both have 29, 14 of which are abdominal, and 15 are caudal elements. In *Chetia flaviventris* the counts are 30-32, mode 31, comprising 14 or 15 (mode 15) abdominal, and 15-17 (modes 16 and 17) caudal centra. Hypurals 1 and 2, and 3 and 4 are apparently fused in the MRAC specimens radiographed; in the holotype all are free, but 3 and 4 are closely apposed. All hypurals are free in the *Chetia flaviventris* material radiographed.

The pharyngeal apophysis of *C. welwitschi* holotype is of the *Haplochromis*-type, and is broad, with a laterally expansive contribution from the parasphenoid; its structure was not examined in the MRAC material. No information is available about the vertebral apophysis for the *retractor arcuum branchialis* muscle.

All three specimens are males and, apparently, are adult. The 146 mm SL fish is sexually active. In none does the first pelvic ray extend posteriorly beyond the anus. This ray in the 146 mm specimen is distinctly longer than the 2nd ray, but it is not filamentous; in the two smaller fishes, the first ray is but slightly longer than the second.

The occurrence and pattern of the numerous anal spots is described above (p. 235). Poll's drawing (1967: fig. 149) of another Angolan specimen shows, in contrast, only three or four spots confined to the posterior part of the soft anal fin. This may be the result of an artist's error stemming from the extreme difficulty one experiences in arranging the lighting to reveal such faintly pigmented areas.

There is some uncertainty about the type locality of *Chetia welwitschi*. Originally recorded as being collected by Welwitsch from Fluilla, Angola (Boulenger, 1898), it was later thought that Fluilla had been a misspelling of Huilla, a town and district in the south-western part

of the country (Bell-Cross, 1975: 427). If that is so, then the holotype would be from the Cunene drainage. With the addition of Poll's material, the range of *C. welwitschi* is now extended to include the Zaire drainage system as well (Poll, 1967: 307).

If the generic placement of *P. welwitschi* is correct, then it is the only Angolan haplochromine, except *Pseudocrenilabrus philander*, belonging to a taxon also occurring in the Limpopo drainage (the type material of *Chetia flaviventris* is from a dam on the Sterkstroom river, a tributary of the Crocodile). That remark is made, of course, on the assumption that the specimens Poll identified as *Haplochromis darlingi* are not referable to the genus *Pharyngochromis*, the genus in which *H. darlingi* is now placed (Greenwood, 1979: 310).

Neither the inclusion of *Pelmatochromis welwitschi* in *Chetia*, nor the discovery of *C. mola*, provide any information on the phyletic relationships of the genus. As Trewavas (1964) suggested, its relationships would seem to be with the *Serranochromis* generic complex, but the characters on which that suggestion was made are still of unproven value in a truly phylogenetic scheme of classification (Greenwood, 1979: 309).

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